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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 77, NO. 2, PP. 63–76 MARCH, 1950

A CYTOLOGICAL STUDY OF SOME TEXAS GRAMINEAE

WALTER V. BROWN

The latest extensive list of chromosome numbers in the Gramineae (Myers 1947) includes data on over 800 species, while chromosome numbers not included in that list (such as those given by Parodi, 1946 and Brown, 1948, together with excluded genera) bring the number of grass species studied cytologically to about 1,000, or at least one-fifth of all the species in the family.

The species investigated in this study are native forage grasses and their close relatives, introduced forage and lawn grasses, as well as native non-forage grasses. A total of eighty species in thirty-eight genera are reported, these genera being distributed in ten tribes. Identification and nomenclature of all United States grasses are according to Hitchcock (1935). Herbarium specimens have been made of the plants studied and microscope slides have been attached to the sheets. Many of the plants are growing in the grass garden of the Plant Research Institute while the herbarium specimens are filed in the University of Texas herbarium.

Material and Methods. Root tips of the grasses were either collected in the field or from potted plants after a period of growth in the greenhouse. After fixation in the CRAF modification of Navashin's fluid, the root tips were embedded and sectioned according to standard procedures and stained with Heidenhain's iron alum-hematoxylin. For meiotic study young inflorescences were fixed in absolute-acetic fixative and kept in 70 percent ethyl alcohol until smeared in aceto- or propionocarmine.

In table 1 the author's collection numbers are listed. In a few cases plants were furnished by the U. S. Soil Conservation Service Station at San Antonio, Texas and their numbers are used and so indicated. In the case of *Andropogon ischaemum* L., the King Ranch strain as grown at San Antonio was studied.

References to previous records of chromosome numbers may be found in the lists of Brown, 1946; Darlington and Janaki Ammal, 1945; Myers, 1947; and Parodi, 1946. If two or more references to the same species exist, only the latest is given unless there are conflicting chromosome numbers reported.

DISCUSSION

Table 1 lists the chromosome numbers obtained. The listing of $2n$ numbers indicates that counts were derived from a study of mitosis in root tips

[THE BULLETIN for January–February (77: 1–62) was issued January 18, 1950]

TABLE 1. Chromosome numbers in the gramineae

Genus and Species	Collection No.	Fig.	n	2n	Previous records	
					2n	Authority
Sitanion hystrix (Nutt.) J. G. Smith	3370	1		28	28	(Stebbins and Love 1941)
Elymus interruptus Buckl.	3484	2 and 3	14	28		
Bromus catharticus Vahl.	3276	4		42	42	(Stebbins and Tobgy 1944)
Uniola laxa (L.) B.S.P.	3422	5		24		
U. sessiliflora Poir.	3431	6		24		
U. latifolia Michx.	3437	7		48	48	(Avdulow 1931)
Triodia pilosa (Buckl.) Merr.	3273 & 3486	8		16		
T. buckleyana (L. H. Dewey) Vasey	3479	9		32		
T. elongata (Buckl.) Scribn.	3480 & 3481	10		32		
T. mutica (Torr.) Scribn.	3314 & 3286	11		32		
T. stricta (Nutt.) Benth.	3410	12		32		
T. albescens Vasey	3237	13		32		
T. texana S. Wats.	3285 & 3296	14		16		
Pappophorun bicolor Fourn.	3320	15		40		
ditto	3291	16		60		
P. mucronulatum Nees	3241	17		60		
Blepharidachne bigelovii (S. Wats.) Hack.	3331	18		14		
Eragrostis secundiflora Presl.	3407	19		40		
E. beyrichii J. G. Smith	3280	20		40		
E. spicata Vasey	SA-4061	21		40		
Vaseyochloa multinervosa (Vasey) Hitch.	3485	22		56		
Agrostis verticillata Vill.	3279	23		14	28	(Sokolovskaya 1938)
Sporobolus virginicus (L.) Kunth.	3247	24		18		
S. neglectus Nash	3402	25		36		
S. cryptandrus (Torr.) A. Gray	3292	26		36	18	(Nielsen 1939)
S. Wrightii Munro.	3242	27		36		
S. asper (Michx.) Kunth	3397 & 3478	28		54		
ditto	3474 & 3476	29		108		
Muhlenbergia lindheimeri Hitchc.	3487	30		20		
M. emersleyi Vasey	3299	31		40		
M. brachyphylla Bush	3328	32		40		

TABLE 1. Chromosome numbers in the gramineae—*(Continued)*

TABLE 1. Chromosome numbers in the gramineae—(*Continued*)

Genus and Species	*Collection No.*	*Fig.*	*n*	*2n*	*Previous records*	
					2n	*Authority*
Brachyelytrum erectum (Schreb.) Beauv.	2838	33		22		
Limnodea arkansana (Nutt.) L. H. Dewey	3489	34	7	.....		
Sphenopholis obtusata (Michx.) Scribn.	3490	35		14		
Tragus berteronianus Schult	3491	36		20		
Hilaria belangeri (Steud) Nash	3394	37		36		
H. mutica (Buckl.) Benth.	3279	38 and 39	18	36		
Leptochloa filiformis (Lam.) Beauv.	3352	40		20		
L. dubia (H.B.K.) Nees	3332	41		60		
Bouteloua chondrosioides (H.B.K.) Benth.	3342	42		14		
B. filiformis (Fourn.) Griff.	3238	43		14		
B. rigidiseta (Steud.) Hitchc.	3455	44		28	35	(Fults 1942)
B. trifida Thurb.	3255	45		28		
B. breviseta Vasey	3336	46		28	21	(Fults 1942)
B. eriopoda (Torr.) Torr.	3275	47		28	21	(Fults 1942)
Schedonnardus paniculatus (Nutt.) Trel.	3383 & 3384	48		30		
Cynodon dactylon (L.) Pers.	4231	49		36	36	
Chloris virgata Swartz	3273	50		20	30	(Krishnaswamy 1940)
					14	(Nielsen and Humphrey 1937)
C. gayana Kunth	3253	51		20	20 & 40	(Moffett 1944)
C. ciliata Swartz	3265	52		40		
C. andropogonoides Fourn.	3278	53 and 54	20	40		
C. verticillata Nutt.	3382	55	40	.....		
C. petraea Swartz	3245	56		40		
C. cucullata Bisch.	3232	57		40	40	(Avdulow 1931)
Astrebla lappacea (Muell) Domin.	T-3679	58		40		
Phalaris caroliniana Walt.	3277	59 and 60	7	14		
Leersia lenticularis Michx.	3443	61	24	.....		
L. monandra Swartz	3272	62	24	.....		
Zizania texana Hitchc.	3454	63 and 64	15	30		

TABLE 1. Chromosome numbers in the gramineae—(*Continued*)

Genus and Species	*Collection No.*	*Fig.*	*n*	*2n*	*Previous records*	
					2n	*Authority*
Axonopus furcatus (Flugge)	3438	65		40		
Stenotaphrum secundatum (Walt.) Kuntze	3275	66		18	18	(Parodi 1946)
					20	(Brown 1948)
Eriochloa contracta Hitchc.	3248	67		36		
Echinochloa colonum (L.) Link	3225 & 3395	68		36	130	(Krishnaswamy 1940)
					72	(Ammal 1945)
Panicum reptans L.	3465	69		14		
P. texanum Buckl.	3464	70		36	36	(Nielsen 1939)
					54	(Burton 1942)
Paspalum plicatulum Michx.	3467	71		20	40	(Saura 1941)
P. urvillei Steud.	3262	72		40	60	(Nielsen 1939)
					40	(Burton 1940)
P. floridanum Michx.	3406	73		120	120	(Brown 1948)
ditto	3418	74		160	160	(Brown 1948)
P. dilatatum Poir.	3267 & 3469	75		40	40	(Burton 1940)
Cenchrus myosuroides H.B.K.	3260	76	27	54	70	(Avdulow 1931)
Setaria macrostachya H.B.K.	3240	77		72		
Sorghastrum Elliottii (Mohr) Nash	3440	78		20	20	(Stebbins in Myers 1947)
S. nutans (L.) Nash	3450	79		40	40	(Church 1929)
Andropogon glomeratus (Walt.) B.S.P.	3401	80		20	20	(Church 1936)
A. cirratus Hack.	3307	81		20		
A. scoparius Michx.	3460	82		40	40	(Church 1940)
A. saccharoides Swartz	3459	83		60	60	(Neilsen 1939)
					100	(Church 1940)
A. barbinodis Lag.	3300	84		80		
A. Hallii Hack.	3274	85		60	60	(Church 1940)
					60	(Nielsen 1939)
ditto	3304	86		100		
A. ischaemum L.	KR	87 and 88	20	40	45	(Krishnaswamy 1940)
Eremochloa ophiuroides (Munro) Hack.	3458	89		18		
Zizaniopsis miliacea Doel. & Asch.	3363		12	24	24	(Brown 1948)

while *n* numbers indicate that the counts were made in a study of the first meiotic division in pollen mother cells. Many of these reported chromosome numbers require little or no comment whereas others are highly significant and will be discussed at greater length.

Hordeae. Two species in the closely related genera *Sitanion* and *Elymus* were studied: *S. hystrix* and *E. interruptus*. *S. hystrix* collected in the Texas Panhandle has $2n = 28$ chromosomes (fig. 1). All chromosome reports of this species agree that it is tetraploid. In *Elymus* a large number of species have heretofore been studied cytologically and so far all American species have proven to be polyploid (Myers 1947). The material of *E. interruptus* studied comes from Llano Co., Texas, where the type was collected. Dr. Stebbins of the University of California has compared this material with the type. Root tips were collected from ten plants and in all cases the chromosome number was 28 (fig. 2). A study of meiosis in three greenhouse-grown plants revealed 14 bivalents at diakinesis, all with at least one chiasma but usually two (fig. 3).

Festuceae. A great diversity in basic chromosome numbers 5, 6, 7, 8, 9, 10, and 12 are found in this tribe as delimited by Hitchcock (1935). Most of these basic numbers were found in this study. The occurrence of multiple basic numbers suggests that this is a very artificial tribe and in any phylogenetic treatment it should be broken up along the lines suggested by Hubbard (1934). The basic number 12 is now well established for *Uniola* with the addition of two more species (figs. 5–7). The genus *Triodia*[1] has, apparently, two basic numbers, 7 and 8 (Myers, 1947 and Parodi, 1946). Covas (1945) reports *Tridens pilosa* var. *mendocina* to have 16 chromosomes and Calder (1937) reports *Triodia thomsonii* to have 48. In both of these cases the basic number is 8. Nielsen and Humphrey (1937) found *Triodia flava* to have 28 chromosomes with a basic number 7. In the present study seven species of this genus were found to have a basic number 8, (figs. 8–14), two species being diploid and five tetraploid. In *T. texana* the complement consists of four short, four long and eight medium length chromosomes (fig. 14) while in other species there is little variation in chromosome length among the 16 or 32 chromosomes. The basic number $x = 8$ is rather rare in the grass family, being found in a few rather specialized genera of the Festuceae: *Pleuropogon*, *Orcuttia* and *Triodia* (Myers 1947). Of these, *Triodia* is the only large genus. It seems probable that in *Triodia* $x = 8$ and has been derived directly from $x = 7$ as found in species of typical Festuceae.

In *Pappophorum* the basic number is 10, agreeing in this with the two closely related genera *Cottea* and *Enneapogon* (Covas 1945). The separation of these genera into the tribe Pappophoreae (Hubbard 1934) seems justified

[1] Parodi favors the generic name *Tridens* but Hitchcock (1935) is followed in this paper.

upon a common basic number of $x = 10$ and upon the uniformly small size of the chromosomes. The two species of *Pappophorum* studied are very similar morphologically and are found to have the same chromosome number, $2n = 60$ (figs. 16 and 17) although one plant of *P. bicolor* was found with $2n = 40$ (fig. 15).

Blepharidachne, which might be considered as in the Pappophoreae, differs cytologically in having a basic number $x = 7$ as well as as in the large chromosomes (fig. 18). Morphologically, too, this genus differs in having a three-nerved lemma rather than a lemma with many nerves. It appears, therefore, that *Blepharidachne* belongs among the typical Festuceae.

The genus *Eragrostis* also has a basic number $x = 10$ and the chromosomes are small. Morphologically and anatomically (Hubbard 1934) the genus shows closer relationship to the Chlorideae than to the Pappophoreae. Hubbard derives the tribes Eragrosteae and Chlorideae from a common stock on the basis of all evidence at hand. In fact, Hubbard's Eragrosteae contains many genera usually included in the Chlorideae. Members of the Eragrosteae represented in this study are: 3 species of *Eragrostis* $x = 10$ (figs. 19–21), 2 species of *Leptochloa* $x = 10$ (figs. 40 and 41) and 7 species of *Triodia* $x = 8$. Previous reports (Myers 1947) give *Eleusine* a basic number $x = 9$ and *Dactyloctenium* probably 8. Although there is considerable variation in basic number all genera agree cytologically in having small chromosomes and in the basic numbers being intermediate within the scale of basic numbers present in the family.

The monotypic south Texas species *Vaseyochloa multinervosa* has previously been included at one time or another in the genera *Melica, Distichlis* and *Triodia* (Hitchcock 1935). These genera have basic numbers 9, 10, and 8 respectively. There is, therefore, evident justification for the establishment of the genus *Vaseyochloa* for the basic chromosome number is found by the present study to be 7. The species is an octoploid with $2n = 56$ (fig. 22).

Agrostideae. Four genera in the tribe were studied. Typically this tribe has large chromosomes and a basic number $x = 7$ as found in *Agrostis verticillata* (fig. 23) and in the monotypic *Limnodea arkansana* (fig. 34). Other genera studied are cytologically distinct in having small chromosomes and basic numbers other than 7. Hubbard places *Sporobolus* in a distinct tribe and states that "It shows close relationship to *Eragrostis* and has probably been derived from that genus." Most species of *Sporobolus* have a basic number $x = 9$ although a few have $x = 10$. If the genus has been derived from *Eragrostis* then there has been a reduction in basic number from 10 to 9. Both genera are found mostly in tropical or warm temperate regions and so differ distributionally from the typical Festuceae and Agrostideae, which are found in temperate or even in arctic regions. All American species of *Sporobolus* have a basic number 9 as was corroborated in this study. Two

cytological forms of *S. asper* were found, one with 54 chromosomes (fig. 28) and a 12-ploid form with 108 chromosomes (fig. 29).

Darlington and Ammal (1945) include *Muhlenbergia* in the Sporoboleae although Hubbard (1934) places it in the Agrostideae. It belongs near *Sporobolus* for both genera are found in the same warm regions of the Americas and cytologically both have small chromosomes with intermediate basic numbers (9 and 10). In *Muhlenbergia* all species studied have $x = 10$. The group Epicampes, sometimes considered a genus, does not differ cytologically from the other species. *M. rigens* (Stebbins and Love 1941), *M. emersleyi* and *M. Lindheimeri,* all of the Epicampes group, have $x = 10$ small chromosomes (figs. 30 and 31).

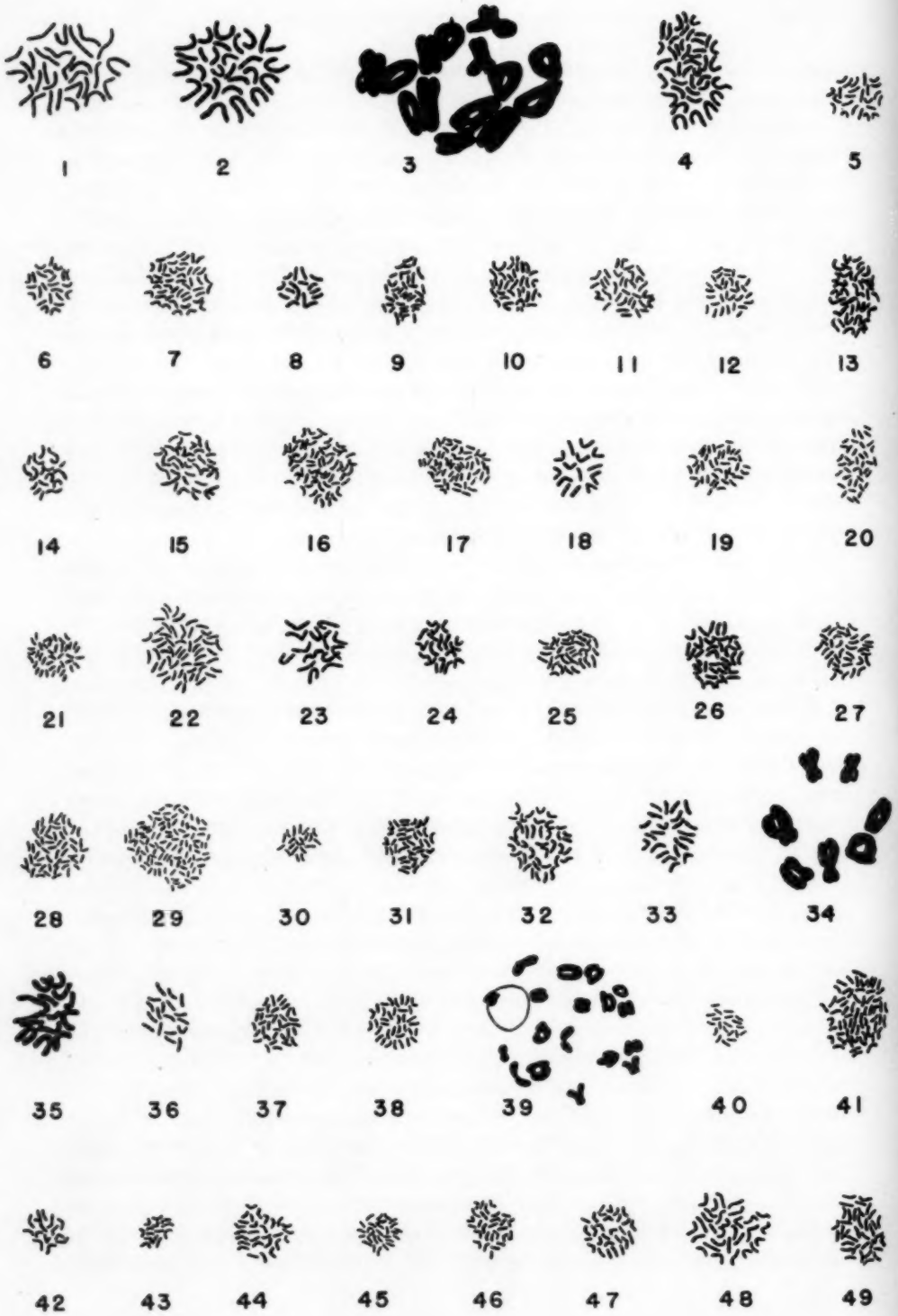
Brachyelytrum erectum a monotypic woodland species of eastern North American evidently belongs close to *Stipa.* Although *Stipa* shows considerable aneuploidy the basic number $x = 11$ has been reported in nearly half of the species studied. *B. erectum* with $2n$ equals 22 (fig. 33) also has $x = 11$. Other genera with x = 11 are *Aristida* and *Piptochaetium.* All show morphological evidences of interrelationship.

Aveneae. One species in this tribe was studied, *Sphenopholis obtusata.* It is cytologically typical of the Aveneae in having large chromosomes and a basic number 7. This is a diploid species (fig. 35) as is *S. intermedia,* the only other species of the genus to have been previously studied (Myers 1947).

Zoysieae. This is a small tribe of tropical and warm temperate, usually dry, regions. In the southwestern United States the genus *Hilaria,* with five species, is of considerable value for forage. *Hilaria belangeri,* curly mesquite grass, is close to the type species whereas *H. mutica* and two other species have been segregated by some taxonomists as a distinct genus *Pleuraphis.* Both *H. belangeri* and *H. mutica* have the same basic chromosome number $x = 9$, and the chromosomes are small.

Previously reported basic numbers in this tribe are 10 in *Tragus* and *Zoysia* and 9 in *Anthephora. Tragus berteronianus* $2n = 20$ (fig. 36) is diploid whereas *T. racemosus* is a tetraploid according to Avdulow (1931).

Chlorideae. In this tribe there are three basic numbers 7, 9, and 10. Two species of *Leptochloa* (fig. 40 and 41) agree with previous reports in the genus that $x = 10$. The position of this genus has been discussed under *Eragrostis. Schedonnardus paniculatus,* a monotypic form, also has a basic number 10 (fig. 48). *Cynodon dactylon,* Bermuda grass, has been reported to have $2n = 36$ (Avdulow 1931) and 30 (Hunter 1934). The present study confirms the count of Avdulow (fig. 49) giving this genus a basic number $x = 9$. The American genus *Bouteloua* has a basic number $x = 7$ in the six species studied. Fults (1942) reported many aneuploid chromosome numbers in this genus. Aneuploidy has recently been confirmed in *B. curtipen-*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dula, while one strain of that species is apomictic (Harlan 1949). The present study although limited in the number of plants of each species studied does not confirm the conclusions of Fults that the species of *Bouteloua* are largely aneuploid. Of the six species studied (figs. 42–47) all are euploid with the basic number $x = 7$. This genus of very valuable forage grasses should be investigated further.

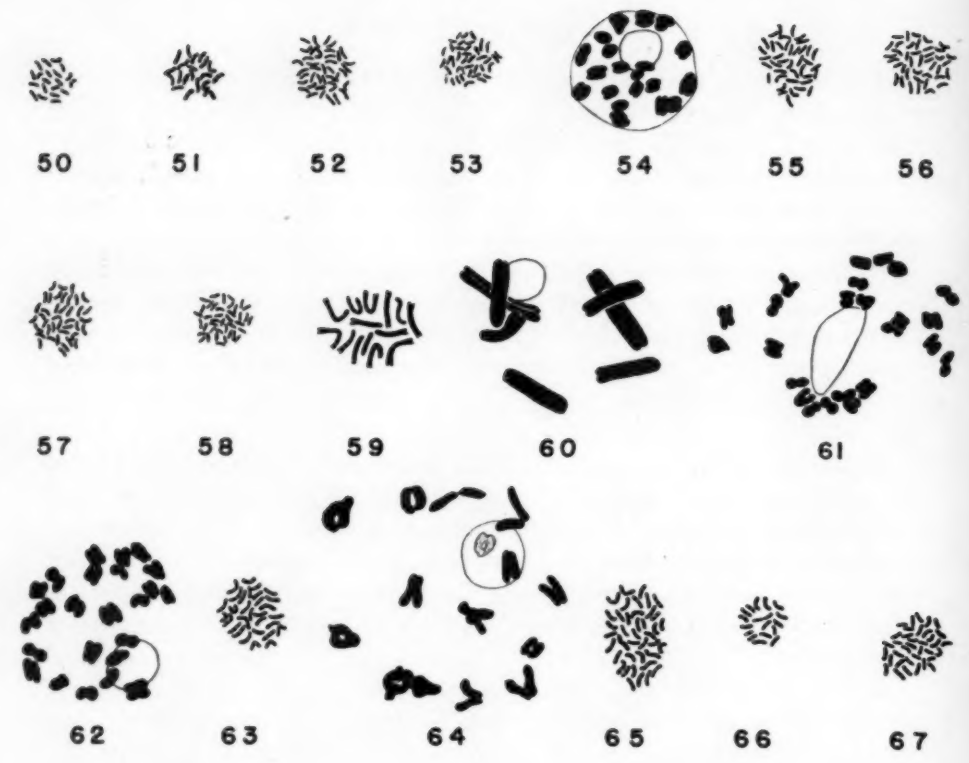
Of the seven species of *Chloris* studied (figs. 50–57) two are diploid and five tetraploid. Previous counts of 14 and 30 for *C. virgata* are unusual in this genus. The present count of $2n = 20$ (fig. 50) fits with the other species studied in giving a basic number $x = 10$. *Astrebla lappacea*, an Australian species of the Chlorideae, is a tetraploid with the basic number $x = 10$ (fig. 58).

Phalarideae, Oryzeae and Zizaneae. *Phalaris caroliniana* (figs. 59 and 60) agrees with most other species of the genus in having a basic number $x = 7$ although two species have been reported to have $x = 6$. The great difference in size between the somatic and meiotic chromosomes of this and six other species is striking. In all cases, the meiotic chromosomes are considerably longer and thicker at diakinesis than are the somatic chromosomes at metaphase.

Leersia lenticularis (fig. 61) and *L. monandra* (fig. 62) agree with three other American species of this genus in having $n = 24$ (Brown 1948). The basic number in the Oryzeae is $x = 12$, as found in *Oryza*, but as yet no species of *Leersia* has been found with $n = 12$. This study completes a survey of the five United States species of this genus.

All species of *Zizania* previously studied have the same chromosome number, $2n = 30$ and a basic number $x = 15$. The local *Z. texana* growing only

FIGS. 1–49. Camera lucida drawings of chromosomes of the following Gramineae. Magnification X 866. FIG. 1. *Sitanion hystrix*, $2n = 28$. FIG. 2. *Elymus interruptus*, $2n = 28$. FIG. 3. *Ditto*, $n = 14$. FIG. 4. *Bromus catharticus*, $2n = 42$. FIG. 5. *Uniola laxa*, $2n = 24$. FIG. 6. *U. sessiliflora*, $2n = 24$. FIG. 7. *U. latifolia*, $2n = 48$. FIG. 8. *Triodia pilosa*, $2n = 16$. FIG. 9. *T. buckleyana*, $2n = 32$. FIG. 10. *T. olongata*, $2n = 32$. FIG. 11. *T. mutica*, $2n = 32$. FIG. 12. *T. stricta*, $2n = 32$. FIG. 13. *T. albescens*, $2n = 32$. FIG. 14. *T. texana*, $2n = 16$. FIG. 15. *Pappophorum bicolor*, $2n = 40$. FIG. 16. *Ditto*, $2n = 60$. FIG. 17. *P. mucronulatum*, $2n = 60$. FIG. 18. *Blepharidachne bigelovii*, $2n = 14$. FIG. 19. *Eragrostis secundiflora*, $2n = 40$. FIG. 20. *E. beyrichii*, $2n = 40$. FIG. 21. *E. spicata*, $2n = 40$. FIG. 22. *Vaseyochloa multinervosa*, $2n = 56$. FIG. 23. *Agrostis verticillata*, $2n = 14$. FIG. 24. *Sporobolus virginicus*, $2n = 18$. FIG. 25. *S. neglectus*, $2n = 36$. FIG. 26. *S. cryptandrus*, $2n = 36$. FIG. 27. *S. Wrightii*, $2n = 36$. FIG. 28. *S. asper*, $2n = 54$. FIG. 29. *Ditto*, $2n = 108$. FIG. 30. *Muhlenbergia Lindheimeri*, $2n = 20$. FIG. 31. *M. emersleyi*, $2n = 40$. FIG. 32. *M. brachyphylla*, $2n = 40$. FIG. 33. *Brachyelytrum erectum*, $2n = 22$. FIG. 34. *Limnodea arkansana*, $n = 7$. FIG. 35. *Sphenpholis obtusata*, $2n = 14$. FIG. 36. *Tragus berteronianus*, $2n = 20$. FIG. 37. *Hilaria belangeri*, $2n = 36$. FIG. 38. *H. mutica*, $2n = 36$. FIG. 39. *Ditto*, $n = 18$. FIG. 40. *Leptochloa filiformis*, $2n = 20$. FIG. 41. *L. dubia*, $2n = 60$. FIG. 42. *Bouteloua chondrisioides*, $2n = 14$. FIG. 43. *B. filiformis*, $2n = 14$. FIG. 44. *B. rigidiseta*, $2n = 28$. FIG. 45. *B. trifida*, $2n = 28$. FIG. 46. *B. breviseta*, $2n = 28$. FIG. 47. *B. eriopoda*, $2n = 28$. FIG. 48. *Schedonnardus paniculatus*, $2n = 30$. FIG. 49. *Cynodon dactylon*, $2n = 36$.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in the San Marcos River of Texas also has $n = 15$ and $2n = 30$ (figs. 63 and 64). *Zizania* is the only genus of the tribe so far studied with $x = 15$, all others have $x = 12$ (Brown 1948). *Zizaniopsis miliacea* of central Texas agrees with North Carolina material in having $n = 12$.

Paniceae. This is one of the largest tribes in the grass family. There are typically two basic numbers, 9 and 10, of which 9 is by far the more common; the two genera *Axonopus* and *Paspalum* being the only genera found to have $x = 10$ (Myers 1947). *Axonopus furcatus* from moist creek banks of east Texas is a tetraploid with $2n = 40$ (fig. 65). In *Paspalum* it is found that the large robust species *P. floridanum* has two highly polyploid forms; one with $2n = 120$ (fig. 73) the other with $2n = 160$ (fig. 74). These same polyploid forms were found in North Carolina (Brown 1948).

Stenotaphrum secundatum, a common lawn grass in Texas ,is found to have $2n = 18$ chromosomes (fig. 66). This agrees with the count of Nunez in Parodi (1946) and disagrees with $2n = 20$ reported by Brown (1948) for Florida material.

In the Paniceae the basic number $x = 7$ has been found only in the genus *Pennisetum* where the basic number $x = 9$ is also found. The same two basic numbers are found in *Panicum* with *P. reptans* a weed in the author's garden having $2n = 14$ (fig. 69). All other species of *Panicum* so far studied have $x = 9$, an example of which is *P. texanum* (fig. 70). These two species are placed by Hitchcock (1935) in the section Fasciculata but as Hitchcock and Chase (1910) state, "*Panicum reptans* is placed in the group Fasciculata because it is more closely allied to the other species of that group than to those of any other group, yet the degree of difference between this and any other species of the group is much greater than between such species as *P. fasciculatum*, *P. arizonicum*, and *P. adspermum*." The cytological evidence also shows a great difference between *P. reptans* $x = 7$, and *P. fasciculatum* (Burton 1942) and *P. texanum* with $x = 9$. Whether $x = 7$ has given

FIGS. 50–89. Camera lucida drawings of chromosomes of the following Graminae. Magnification ×866. FIG. 50. *Chloris virgata*, $2n = 20$. FIG. 51. *C. gayana*, $2n = 20$. FIG. 52. *C. ciliata*, $2n = 40$. FIG. 53. *C. andropogonoides*, $2n = 40$. FIG. 54. *Ditto*, $n = 20$. FIG. 55. *C. verticillata*, $2n = 40$. FIG. 56. *C. petraea*, $2n = 40$. FIG. 57. *C. cuculata*, $2n = 40$. FIG. 58 *Astrebla lappacea*, $2n = 40$. FIG. 59. *Phalaris caroliniana*, $2n = 14$. FIG. 60. *Ditto*, $n = 7$. FIG. 61. *Leersia lenticularis*, $n = 24$. FIG. 62. *L. monandra*, $n = 24$. FIG. 63. *Zizania texana*, $2n = 30$. FIG. 64. *Ditto*, $n = 15$. FIG. 65. *Axonopus furcatus*, $2n = 40$. FIG. 66. *Stenotaphrum secundatum*, $2n = 18$. FIG. 67. *Ereochloa contracta*, $2n = 36$. FIG. 68. *Echinochloa colonum*, $2n = 36$. FIG. 69. *Panicum reptans*, $2n = 14$. FIG. 70. *P. texanum*, $2n = 36$. FIG. 71. *Paspalum plicatulum*, $2n = 20$. FIG. 72. *P. urvillei*, $2n = 40$. FIG. 73. *P. floridanum*, $2n = 120$. FIG. 74. *Ditto*, $2n = 160$. FIG. 75. *P. dilatatum*, $2n = 40$. FIG. 76. *Cenchrus myosuroides*, $n = 27$. FIG. 77. *Setaria macrostachya*, $2n = 72$. FIG. 78. *Sorghastrum Elliottii*, $2n = 20$. FIG. 79. *S. nutans*, $2n = 40$. FIG. 80. *Andropogon glomeratus*, $2n = 20$. FIG. 81. *A. cirratus*, $2n = 20$. FIG. 82. *A. scoparius*, $2n = 40$. FIG. 83. *A. saccharoides*, $2n = 60$. FIG. 84. *A. barbinodis*, $2n = 80$. FIG. 85. *A. Hallii*, $2n = 60$. *Ditto*, $2n = 100$. FIG. 87. *A. ischaemum*, $2n = 40$. FIG. 88. *Ditto*, $n = 20$. FIG. 89. *Eremochloa ophiuroides*, $2n = 18$.

rise to $x = 9$ as found in all other species of the genus or whether the $x = 7$ of *P. reptans* has been derived from $x = 9$ by the loss of two chromosomes is not known. If the latter is true it could be an isolated case and so have little phylogenetic significance. If $x = 9$ has been derived from the $x = 7$, then *P. reptans* may relate the rest of the genus to some other group of grasses that has typically a basic number $x = 7$.

Cenchrus myosuroides, reported by Avdulow (1931) to have $2n = 70$, was found in the material studied to have $n = 27$ (fig. 76). This gives it a basic number $x = 9$ typical of most Paniceae. The report of Avdulow may well represent a chromosomal form of the species, for the counts reported by him are usually very reliable. Aneuploidy does exist in the genus (Brown 1948) with a secondary basic number $x = 17$ derived by the loss of a pair of chromosomes from $2n = 36$ giving $2n = 34$.

Andropogoneae. The Asiatic species *Andropogon ischaemum* shows great promise as a forage grass in Texas. A sample of seed from the Soil Conservation Service was planted and thirty plants selected. All plants showed 40 somatic chromosomes (fig. 87). Krishnaswamy (1940) reported this species to have $2n = 45$ but his drawing of the chromosome complement shows 40 chromosomes (p. 11, abb. 6). A study of meiosis in pollen mother cells showed 20 chromosomes (fig. 88). There is some irregularity indicated by univalents and a trivalent but this is probably due to environmental conditions. The material was taken in February, 1949, from plants blooming in the greenhouse. Under these conditions great meiotic irregularity was found, resulting in complete sterility although the same plants grown out-of-doors and blooming in the summer set abundant seed.

Eremochloa ophiuroides, an introduced lawn grass, is a diploid species with $2n = 18$ (fig. 89). It therefore belongs to the small group of genera of Andropogoneae with the basic number $x = 9$; *Rotboellia*, *Manisuris*, and *Arthraxon*.

SUMMARY

The chromosome numbers of 80 species in 38 genera of Gramineae are reported. Of these the chromosome numbers of 52 species are reported for the first time. The basic chromosome number $x = 8$ which is very unusual in the Gramineae is confirmed in the genus *Triodia*. The basic number in the genus *Pappophorum* and its allies is 10 and the chromosomes are small, thereby setting this group off from the typical Festuceae. *Eragrostis* and its allies are cytologically very close to the Chlorideae, both groups having small chromosomes and basic numbers 9 and 10. The monotypic *Vaseyochloa multinervosa*, which at different times has been placed in the genera *Melica*, *Distichlis* and *Triodia*, is cytologically distinct from these genera in having a different basic chromosome number. The group Epicampes of *Muhlen-*

bergia is cytologically indistinguishable from the other species of that genus. The monotypic *Brachyelytrum erectum* shows cytological relationship to *Stipa* and its allies, having a basic number $x = 11$. The basic number in the genus *Hilaria* is $x = 9$. No aneuploidy was found in the six species of *Bouteloua* studied although previous workers report its occurrence. With the study of *Leersia lenticularis* and *L. monandra* it is found that all United States species of this genus have the same chromosome number, $n = 24$. *Zizania texana* like all other species of the genus has $n = 15$ chromosomes. *Panicum reptans* has a basic number $x = 7$ and is the only species in the genus so far studied cytologically to have a basic number other than $x = 9$. *Eremochloa ophiuroides* with $x = 9$ is the fourth genus in the Andropogoneae with this basic number.

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MORPHOLOGICAL EFFECTS OF THYMOL AND RELATED COMPOUNDS UPON THE GERMINATION OF FUNGUS SPORES

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Although a vast amount of experimental work has been devoted to the inhibition of germination and growth of fungi by chemical means, relatively little is known concerning the influence of various chemicals in the induction of changes in organisms thus inhibited. The subject is not even mentioned in a recent and authoritative book on fungicides (Horsfall, 1945). In experiments with thymol and related materials which inhibit growth of Aspergilli and Penicillia, some rather striking effects upon the morphology of germinating conidia were noted, and these observations provide the basis of the present report.

The antifungal activity of thymol (3-hydroxy-para-cymene) and carvacrol (an isomer of thymol) was apparently discovered by Myers (1927), who reported that these substances were fungicidal to an unidentified yeast. Shortly thereafter, Kingery and Adkisson (1928) established that thymol in a concentration of one part in 7500 is fungistatic to various dermatophytes, to *Sporotrichum schenckii,* and to *Coccidioides immitis.* In a previous paper (Wolf and Wolf, 1950), it was found that the growth of a number of Aspergilli and Penicillia was inhibited by thymol and related materials when present in concentrations of 0.025%. The substances tested, in addition to thymol, included carvacrol and "Stabilizer #1" (a mixture of monoisopropyl meta and para cresols, produced by the Sindar Corporation, New York, and intended for use as a mold inhibitor for industrial starches).

Materials and Methods. The fungi studied in the experiments to be reported included cultures of *Aspergillus niger* van Tieghem, *A. sydowi* Bainier and Sartory, *Penicillium crustosum* Thom, *P. cyaneum* Bainier and Sartory, *P. cyclopium* Westling, *P. olivino-viride* Biourge, and *P. waksmani* Zaleski. The medium employed was a modified Czapek's solution containing $NaNO_3$, 3.0 gm.; KH_2PO_4, 1.0 gm.; $MgSO_4 . 7H_2O$, 0.5 gm.; KCl, 0.5 gm.; $FeCl_3$, trace; and sucrose, 30.0 gm. per liter, having a pH of 4.5. The cultures were incubated at room temperature.

Observations. During previous experiments, in which it was sought to determine the thymol concentrations fungistatic to a number of organisms,

[1] From work undertaken in cooperation with the Quartermaster Food and Container Institute for the Armed Forces. The opinions or conclusions contained in this report, No. 282, are those of the authors. They are not to be construed as necessarily reflecting the views or endorsement of the Department of the Army.

difficulty was experienced in some instances in determining whether the small amounts of fungus material present represented new growth or ungerminated inoculum. But upon microscopic examination, it was noted that the spores in certain cultures had become greatly enlarged. It is well known, of course, that a moderate increase in spore size is involved in normal germination. The amount of swelling observed in the presence of thymol, however, was greatly in excess of that consequent upon normal germination, and thus was mainfestly pathological.

Such pathological enlargement of conidia was noted in all species of Penicillium and Aspergillus examined; namely, *Penicillium crustosum*, *P. cyaneum*, *P. cyclopium*, *P. olivino-viride*, *P. waksmani*, *Aspergillus niger*, and *A. sydowi*. The swelling phenomenon thus appears to be a general response and is not restricted to a particular fungus species.

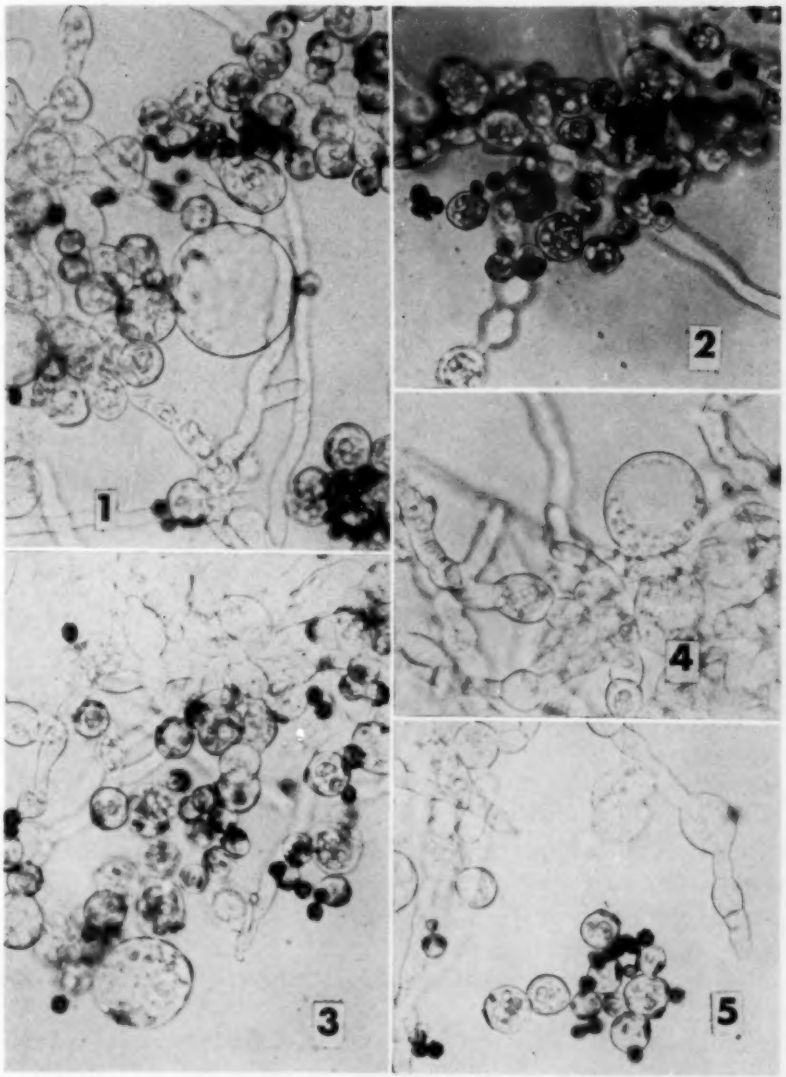
Aspergillus niger, because of its distinctive spores, was selected as a test organism for further inquiry into the swelling phenomenon. As described by Thom and Raper (1945), the conidia in this species are usually 2.5–4 microns in diameter, occasionally reaching 5 microns. The spore wall is rough or spinulose, owing to the deposition of a black pigmented material (aspergillin) in the form of tubercles, bars, or loops, between the outer primary and the inner or secondary wall.

In the presence of thymol, the swollen conidia of *Aspergillus niger* are usually 15–20 microns in diameter. A few may be much larger, the largest observed being 32 microns in diameter. Such extreme enlargement represents an increase in volume of approximately 500 times that of normal conidia. The proportion of swollen spores, however, never approached 100 per cent, since a considerable number always failed to germinate. The outer spore wall (exospore) breaks irregularly, as a result of spore enlargement. In consequence, the black, pigmented material, originally deposited between the outer and inner spore walls, may slough off, or may remain attached at one side of the spore. The appearance of swollen conidia, contrasting normal and abnormal ones in the same field of view, may be seen in figures 1–5.

To determine the relation of swelling to thymol concentration, Czapek's medium was prepared to contain thymol in concentrations ranging from 0.005 to 0.1 per cent. Controls lacking thymol were provided for study of normal germination. Examination of amounts of growth and spore morphology, after one week's exposure to thymol, gave the results presented in table I.

It is apparent from the data included in table I that the swelling of *A. niger* conidia in the presence of thymol occurs only within a restricted range of thymol concentrations.

After exposure to thymol for one week, conidia were removed from the thymol-containing culture solutions, washed thoroughly in several changes



FIGS. 1–5. *Aspergillus niger*. Conidia germinated in the presence of 0.025% thymol. Ungerminated conidia are small, black, and coarsely spiny. Greatly swollen conidia and germ tube cells result from exposure to thymol. Fragments of the exospore wall appear as black patches on swollen conidia.

of distilled water, and transferred to tubes of Czapek's agar. It was found that no growth occurred following exposure to thymol in concentrations of 0.05% or in greater concentrations. Growth occurred, however, in the case of spores previously exposed to 0.025% thymol, indicating that at least some of them were still viable. When these findings are considered in relation to the

data relating swelling to thymol concentration, a coincidence between fungistatic concentrations and those causing swelling is to be noted, suggesting the possibility of interrelation of these two phenomena.

Experiments with carvacrol and "Stabilizer #1" disclosed that swelling is not specifically induced by thymol, but may be produced by either carvacrol or "Stabilizer #1" in concentrations of 0.015–0.025%. In these experiments, however, the percentage of swollen spores was not as high, and the degree of swelling was not as great as that produced by thymol in equivalent concentrations.

Attempts to interfere with swelling by increase in the osmotic pressure of the culture solution were made by adding varying amounts of sodium chloride to Czapek's solution containing 0.025% thymol. With NaCl concentrations of 3% or less, the percentages of swollen spores obtained approximated those noted in the absence of salt. When the NaCl concentration was raised to 4% or higher, however, swelling did not occur.

TABLE I. *The relation of thymol concentration to growth and abnormal swelling of conidia of Aspergillus niger.*

Thymol concentration, %	Amount of growth	Percentage of abnormally swollen conidia
0 (Control)	very abundant	none
0.005	" "	"
0.01	moderate growth	50–60%
0.025	none	10–20%
0.05	"	none
0.1%	"	"

Discussion. The effect of thymol, carvacrol, and "Stabilizer #1" upon the conidia of *Aspergillus niger* appears to be comparable with the findings of Kiesel (1913), who reported abnormal swelling of spores of this fungus in solutions of various acids and acid salts. In M/300 disodium arsenate, an occasional spore measuring 50 microns in diameter was noted by this investigator.

McCallan and Wilcoxon (1934) noted that 1.0 millimolar solutions of sodium tungstate invariably induced the formation of a large spherical vesicle in the germ tube of *Pestalotia stellata*.

Brian, Curtis and Hemming (1946, 1949) have recently established that the "curling factor," produced by *Penicillium janczewskii* and chemically identified as griseofulvin, $C_{17}H_{17}O_6Cl$, markedly affects the morphology of germ tubes of *Botrytis allii*, causing stunting, distortion, excessive branching, and waving or curling of the hyphae. The percentage germination and time required for germination in their experiments, however, were unaffected by variations in the concentration of the active material.

Since swelling of conidia of *A. niger*, induced by the agency of thymol, can be prevented by a concentration of sodium chloride which is non-toxic *per se*, it is clear that the action of thymol upon fungus spores involves alteration of permeability or osmotic properties. The finding that spore enlargement accompanies fungistasis, as evidenced by the occurrence of swelling at thymol concentrations approaching the fungistatic level, suggests that fungistasis is the result, and that osmotic disturbance is the mechanism of the antifungal activity of thymol.

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SUMMARY

Thymol, carvacrol, and "Stabilizer #1" (a mixture of isopropyl meta and para cresols) are fungistatic to *Aspergillus niger*, *A. sydowi*, *Penicillium crustosum*, *P. cyaneum*, *P. cyclopium*, *P. olivino-viride*, and *P. waksmani* in concentrations approximating 0.025%. These materials produce visible morphological changes in germinating fungus spores, studied chiefly in *Aspergillus niger*, which are evident as pronounced enlargement or abnormal swelling of the conidia. Such changes occur only within a narrow range of concentrations of these materials which coincides closely with their fungistatic dosages. It is therefore suggested that the mechanism of fungistasis by thymol and related substances involves alteration in osmotic and permeability characteristics of the spores.

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NOTES ON SOME PACIFIC MEXICAN DICTYOTACEAE[1]

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The subdivisions *Dilophus* and *Pachydictyon* of the old genus *Dictyota,* proposed by J. G. Agardh in 1894, have generally been accepted by phycologists with the notable exception of Setchell and Gardner who felt that the "difficulties in the line of cleavage" did not justify their recognition of these genera in their 1925 account of the Pacific North American Melanophyceae. Taylor also, in 1945, followed Setchell and Gardner with the statement ". . . it appears more difficult to distinguish *Dilophus* from *Dictyota* in the Pacific flora than in the Caribbean," although he recognized *Dilophus* in his 1942 account of the Caribbean marine algae.

The following represents a review of the species of Pacific North America which may properly be identified under any of these three generic names. All of them are of Mexican occurrence. It has seemed practical in this study to distinguish all three genera. The "difficulties in the line of cleavage" have for the present been appreciably subdued with regard to the Pacific Coast flora.

All of the specimens cited are deposited in the Herbarium of the Allan Hancock Foundation unless otherwise indicated.

KEY TO THE PACIFIC NORTH AMERICAN SPECIES OF DICTYOTA, DILOPHUS AND PACHYDICTYON

1. Thallus with a monostromatic medulla, usually distromatic at the margins, and a di-polystromatic cortex, particularly at the margins. *Pachydictyon Binghamiae.*
1. Thallus with a monostromatic cortex and a polystromatic medulla. 2 *(Dilophus.)*
1. Thallus normally with a monostromatic medulla and monostromatic cortex. 3 *(Dictyota.)*
2. Thallus semi-prostrate, pinnately branched, the margins thin, tapered. *Dilophus pinnatus.*
2. Thallus erect, dichotomously branched, the margins thickened, selvage-like. *Dilophus Okamurai.*
3. Blades entire. 5
3. Blades with indeterminate marginal proliferations. *Dictyota dichotoma* (in part).
3. Blades with determinate marginal dentations. 4
3. Blades with deciduous marginal leaflets. *Dictyota Masonii.*
4. Plants rather large, with broad blades, tending toward pinnate branching, with scattered teeth. *Dictyota cribrosa.*
4. Plants smaller, dichotomously branched, the teeth normally abundant and evenly distributed. *Dictyota crenulata.*

[1] A contribution from the Allan Hancock Foundation. The collections upon which this study is based were in part obtained during tenure of a John Simon Guggenheim Foundation Fellowship for which the author expresses grateful acknowledgement.

5. Plants entangled, the lower segments moderately broad but the upper nearly filiform, the angles very wide, commonly over 90°. *Dictyota divaricata*
5. Plants without extraordinary reduction in branch width or particularly divergent branching. 6
6. Axils narrower, internodes proportionally shorter, blades usually over 3.5 mm wide, the apices little reduced. *Dictyota flabellata*
6. Axils wider, internodes proportionally longer, blades often narrower or the apices reduced. *Dictyota dichotoma* (in part)

Pachydictyon Binghamiae (J. Agardh) Dawson, comb. nov. *Dictyota Binghamiae* J. Agardh 1894, p. 72; Collins, Holden & Setchell 1898, "note" to no. 85; Collins, Holden & Setchell 1907, no. 1392; Setchell & Gardner 1925, p. 652. *Dictyota Kunthii* Agardh, as interpreted by Farlow (1876, p. 705) with regard to California specimens only; Farlow, Anderson & Eaton 1878, no. 93. *Glossophora Kunthii* (Agardh) J. Agardh, as interpreted by Collins, Holden & Setchell 1895, no. 85. *Glossophora coriaceum* Holmes 1896, p. 251. *Pachydictyon coriaceum* (Holmes) Okamura 1899, p. 105. *Dictyota Johnstonii* Setchell & Gardner 1924, p. 730; Dawson 1944, p. 228, in part.

The decision by Setchell and Gardner in 1925 to recognize only the older, broader genus *Dictyota*, rather than the several divisions proposed by J. G. Agardh, has directed attention away from the similarity between the common plant of California long known as *Dictyota Binghamiae*, and the *Pachydictyon coriaceum* of Japan. Furthermore, their separation of *D. Binghamiae* from *D. Johnstonii* of the Gulf of California on such an unreliable character as size, has, in the absence of adequate comparative material left the understanding of *D. Johnstonii* in a confused state.

Collections have now been assembled and examined which appear convincingly to show that *Pachydictyon coriaceum* of Japan, *Dictyota Binghamiae* of California, and *D. Johnstonii* of the Gulf of California, actually represent but one species in Nature. In habit, authentic Japanese specimens of *P. coriaceum* are virtually identical with specimens from California and Pacific Baja California of *D. Binghamiae*, and a Japanese plant from Waga, Shima Province is an almost perfect match for the type specimen of *D. Johnstonii* from the Gulf of California. In transverse section all three of these show a prominent monostromatic medulla which is usually doubled or irregularly divided along the margins, and a di-tristromatic marginal cortex which is usually more or less distromatic across the width of the blade. The very dark brown color of the thallus is a character typical of all three as is also the somewhat stupose base. There appears to be no clear distinction in the disposition of the oogonial sori among these several plants. Although both the Japanese and California plants become quite large in size, to 40 cm. high, those of the Gulf of California thus far found have not exceeded 16 cm. in height. All of these should now be embraced by the name *Pachydictyon Binghamiae*.

The fact that Setchell and Gardner (1925) admitted a difficulty in distinguishing *Dictyota Binghamiae* from *D. flabellata*, and the fact that both the description of *D. Binghamiae* J. Agardh and that of *Dilophus flabellatus* Collins take into account the presence of "teeth" on the margins of the frond of the former, has led to the necessity of ascertaining again the identity of the type of *D. Binghamiae* with the California plants known by that name. Accordingly, a typical sample of our California plant, in habit and structure completely in accord with the Japanese *Pachydictyon coriaceum*, was sent to Dr. Harald Kylin for comparison with the Agardhian type. He did so with the comment: "I cannot find any difference between them. The marginal teeth belong only to older parts of the thallus and are quite irregular, present or not present. Your plant is *D. Binghamiae* J. Ag." Since true dentations do not occur on the California plants examined by the author, it may be assumed that the "teeth" mentioned by J. Agardh and remarked by Kylin are abnormal features of his particular specimen and not to be taken into taxonomic account henceforth.

A further complication concerns *Dictyota Johnstonii* in the Gulf of California. This has arisen because of the erroneous original description of *Dictyota hesperia* Setchell & Gardner, also from the Gulf, and the consequent confusion of these two plants by Dawson (1944). As will be shown below, *D. hesperia* is synonymous with *D. flabellata* (Collins) Setchell & Gardner, and a review of the five collections cited by Dawson (1944) under *D. Johnstonii* (other than the type) shows they are referable rather to *D. flabellata*. Recent collections, however, contain specimens conspecific with the type of *D. Johnstonii* and further confirm the identity of these Gulf plants with *Pachydictyon Binghamiae* which is more abundant on the outer Pacific Coast. In the Gulf these plants have been obtained only from sublittoral habitats, while *D. flabellata* in the same region is typically an intertidal species.

Pachydictyon Binghamiae on the Pacific American coast is seen to be of wide distribution. From north to south, some of the known localities of its occurrence are indicated by the following collections: *Doty 4977*, North Bay, Cape Arago, Coos Bay, Oregon, July 1942; *Loomis 10/14/44*, Moss Beach, San Mateo Co., Calif.; *Martin 2/25/45*, Malabu Cove, Santa Monica Bay, Calif.; *Cooper 219*, Palos Verdes headland, Los Angeles Co., Calif., Nov. 1943; *Dawson 4914*, Santa Catalina Island, Calif., March 1948; *Dawson 2431*, La Jolla, San Diego Co., Calif., July 1946; *Dawson 4235a*, south island, Islas Coronados, Baja Calif., Mexico, June 1947; *Dawson 1108*, Bahia de Todos Santos, Baja Calif., April 1946; *Dawson 54*, Cabo Colnett, Baja Calif., Jan. 1946; *Hubbs 46–210*, Islas San Benitos, Baja Calif., Aug. 1946; *Dawson 2876*, Punta Santa Rosalia, Baja Calif., Oct. 1946; *Dawson 2962*, Desembarcadero de Miller, Baja Calif., Oct. 1946; *Taylor 613*, Bahia Thurloe, Baja Calif., March 1934; *Taylor 599*, Cabo San Lazaro, Baja Calif., March 1934; *Dawson 18–40*, Bahia Santa Maria, Baja

Calif., Jan. 1940; *Dawson 6682*, southern tip of Isla Magdalena, Baja Calif., March 1949; *Johnston 81*, Isla Partida, Gulf of California, July 1921; *Dawson 896,966*, Bahia Agua Dulce, Isla Tiburon, Gulf of California, Feb. 1946.

The specimens from Islas Secas, Panama, *Schmitt 456c-33*, cited under *Dictyota Binghamiae* by Taylor, 1945, do not have the structure of this species and must be referred elsewhere.

Use of the generic name *Pachydictyon* for this species following the interpretation of Okamura is made with some hesitation, since the type of the genus, *Pachydictyon furcellatum* (Harv.) J. Agardh is a very dissimilar plant, probably not of close natural relationship. We have, however, two precedents, in the work of J. Agardh himself, and in that of Okamura, in the application of one of the other generic segregates of the old genus *Dictyota*. J. Agardh described *Dilophus marginatus* (1894, p. 91) from New Holland in which the characters of *Dilophus* are assumed only at the margins of the thallus. Later, Okamura (1913, p. 33) having described a *Dictyota marginata* of similar characters from Japan, transferred it to *Dilophus* (1915, p. 154) but considered it distinct from *D. marginatus* J. Agardh, as did also Yendo (1916, p. 252) who reduced it under *Dilophus flabellatus* Collins. Okamura, in 1934 (p. 883) again revived his *Dilophus marginatus* and recognized it as distinct, but without a new name. By Okamura (1936, p. 167) and in subsequent Japanese literature this plant has been recognized simply as *Dilophus marginatus* (non J. Ag.) Okamura. To clarify the record it is necessary now to propose a new name for this plant:

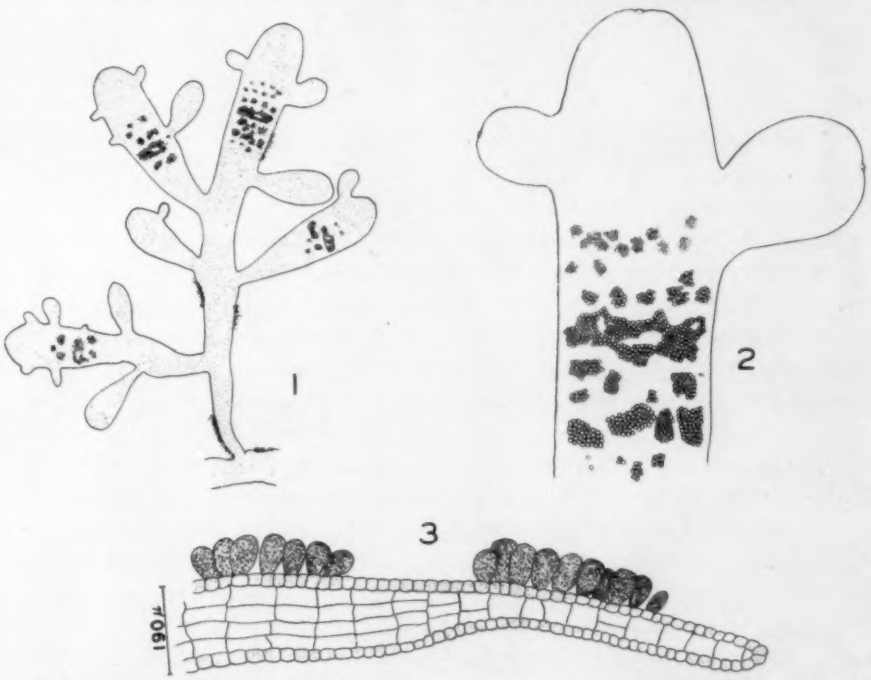
Dilophus Okamurai Dawson, nom. nov. *Dictyota marginata* Okamura 1913, p. 33. *Dilophus marginatus* (Okamura) Okamura 1915, p. 154; 1934, p. 883; 1936, p. 167. *Dilophus flabellatus* Collins, as to Japanese specimens interpreted by Yendo 1916, p. 252.

In accord with the foregoing, in the application of *Pachydictyon* to *Dictyota Binghamiae*, we recognize the same degree of distinction from the old genus *Dictyota* as in the application of *Dilophus* to *D. marginatus* J. Agardh and *D. Okamurai* Dawson. In the one case, the medulla is thickened at the margins and the cortex is left unmodified; in the other case, the cortex is thickened, particularly at the margins, and the medulla left unmodified or only slightly so.

Surprisingly, recent field work in the region of Cabo San Lucas, Baja California (March 1949), has brought to light specimens which appear identifiable with *Dilophus Okamurai*. Two ample collections, *Dawson 6857*, dredged in 10 fms. in Bahia de San Lucus, and *Dawson 6792*, from intertidal pools at Cabeza Ballena, represent a plant which, except for somewhat smaller size, is indistinguishable from the Japanese plant. These specimens have the peculiar stoloniferous bases bearing distinctly stipitate blades with

conspicuously thickened margins. The stoloniferous portions are somewhat stupose and the dichotomous blades in proportions and angle of branching are quite identical with the Japanese plant as illustrated by Okamura, though the Mexican specimens at hand are mostly but half the size indicated for *D. Okamurai*. Well developed reproductive material has not been found in the Mexican collections.

Dilophus Pinnatus Dawson, sp. nov. figs. 1–3. Plantis semiprostratis, parte libera 1–2 cm longa, complanata, spatulata, semel vel bis pinnatim ramosis, segmentis 1–2 mm latis; thallo 150–220 μ crasso margine graciliore,



FIGS. 1–3. *Dilophus pinnatus* Dawson, from the type collection, *Dawson 3691*, Miramar, Nayarit, Mexico. FIG. 1. Portion of a mature plant, × 2.5. FIG. 2. Detail of apical portion of a plant to show oogonial sorus, × 8.5. FIG. 3. Transverse section of a blade through an oogonial sorus to show medullary structure.

in parte centrali medulla 3–5 stratosa donato; cortice 1-stratoso; oogoniis 90–100 μ longis, 70–80 μ diam. in soris densis irregularibus segmentis terminalibus fultis.

Plants semi-prostrate, the lower parts entangled and attached to other small turf-forming algae by means of marginal rhizoidal outgrowths; free parts 1–2 cm. long, complanate, spatulate, once or twice pinnately short-branched, the segments 1–2 mm. wide, broadly rounded at the apices; thallus in transverse section 150–220 μ thick in the mid-parts, tapering to 100 μ at the margins, of three cell-layers, the medulla composed of colorless, rec-

tangular cells in 3–5 (usually 4) strata in the mid-portions, 1–2, at the margins; cortex unistratose, of densely pigmented ovate cells 20–25 μ diam.; oogonia ovoid, 90–100 μ long, 70–80 μ in diam., deeply pigmented, produced in dense irregular sori on both sides of the broad, terminal parts of the thalli, the sori containing 30–200 oogonia; antheridia and aplanospores not seen.

TYPE: *Dawson 3691,* growing in mats of small algae on a cobblestone shore at Miramar, Nayarit, Mexico, December 20, 1946. Herb. A. Hancock Foundation 36929.

This species is amply distinct from all other species of *Dilophus* heretofore described by manner of its small size and entangled habit combined with its unusual manner of pinnate branching.

DICTYOTA CRIBROSA Setchell & Gardner, 1930, p. 147; *Dictyota flabellata* (Collins) Setchell & Gardner, as interpreted by Setchell & Gardner (1925, p. 652) with respect to Monterey, California specimens only; Smith 1944, p. 101; Doty 1947, p. 34.

From time to time there has been found in beach drift at Monterey, California a large *Dictyota* of size and habit similar to *Pachydictyon Binghamiae,* but with the thin blades and monostromatic medulla of *D. flabellata.* These plants have usually been identified hesitatingly with *D. flabellata* with which, however, they are not identical. Additional examples of this plant have appeared recently from widely scattered collections, all from dredgings or sublittoral drift, from Oregon to Cortez Bank off southern California. These plants are all alike in having a monostromatic cortex, a tendency toward pinnate branching, and in possessing occasional well-defined marginal teeth. Such marginal teeth are known heretofore only in *D. cribrosa* of Isla Guadalupe, Baja California, Mexico, and an examination of the type of that species shows that all of the plants indicated above may quite plausibly be identified under that name. The fact that the type has somewhat longer and more frequent teeth than the other collections at first disinclined the author from accepting their identity, but a recent collection from Isla Guadalupe contains a young specimen of *D. cribrosa* with the teeth widely scattered and disposed similarly to those of the California and Oregon material. Awaiting confirmation from additional, fully mature material from Isla Guadalupe, it appears practical to consider all of these dentate specimens of sublittoral origin under the name *D. cribrosa* Setchell & Gardner.

Material examined: *Doty 5056,* North Bay, Cape Arago, Coos Bay, Oregon, July 1942; *Westfall,* 1892, Pacific Grove, Calif. (Herb. U.C. 264818); *Gardner 6495,* Carmel Bay, Calif., May 1928 (Herb. U.C. 392847); *AHF Sta. 1431–41,* White Cove, Santa Catalina Island, Calif., Sept. 1941; *AHF Sta. 1336–41,* Cortez Bank, Calif., June 1941; *Hubbs 46–153,* Isla Guadalupe, Baja Calif., Mexico, Dec. 1946.

DICTYOTA CRENULATA J. Agardh, 1847, p. 7; Setchell & Gardner 1924, p. 730; 1925, p. 655; Dawson 1944, p. 228; Taylor 1945, p. 90.

This is a common species of Pacific Mexico and Central America which

seems to reach its northern limit somewhere near the southern end of Baja California. It is of exceptional abundance in some areas of the Gulf side of the Cape District of Baja California where it is often cast up on the shore in large masses mixed with *Dictyota divaricata* Lamouroux. In its typical form it is readily recognized by its regularly and prominently dentate margins, but in some instances plants occur in which the dentations are very much reduced, or at times almost absent. A large sample from Bahia de La Paz, *Dawson 3472*, November 1946, shows a range from plants with strong, regular dentations to those with but a few scattered teeth near the base of otherwise entire blades. The plant illustrated by Taylor (1945, *pl. 10*) from the Revillagigedo Archipelago represents a form with somewhat broader, shorter terminal segments than occur in most of the Baja California specimens.

DICTYOTA FLABELLATA (Collins) Setchell & Gardner 1924, p. 12; Setchell & Gardner 1925, p. 652, in part. *Dilophus flabellatus* Collins in Collins, Holden & Setchell 1901, no. 834. *Dictyota hesperia* Setchell & Gardner 1924a, p. 731; Dawson 1944, p. 228. *Dictyota Johnstonii* Setchell & Gardner, as interpreted by Dawson 1944, p. 228, excluding type.

An examination of Collins' original description of this species indicates that he was distinguishing his new species from *Dictyota Binghamiae* mainly on the basis of J. Agardh's description of the latter. In following J. Agardh's diagnosis which mentions the "more or less frequent acute, incurved, marginal teeth," Collins used this character as one separating his *Dilophus flabellatus* from *D. Binghamiae*, but it appears also that in his study he must have confused small examples of *Pachydictyon Binghamiae* with his plant, especially lighter colored antheridial ones, for he mentions the more frequent occurrence of a divided cortex in antheridial plants. The reexamination of several co-type specimens of *D. flabellata* in P.B.A. no. 834 has failed to reveal a doubling of the cortex or of the medulla in any of them, even at the margins. Young examples of *Pachydictyon Binghamiae*, however, which may at times be superficially indistinguishable from *D. flabellata*, regularly show clearly this more complex internal structure.

Since, from the examination of a large series of specimens of *Dictyota flabellata*, it appears that the doubling of the cortex and more particularly of the medulla is rare and atypical, and that the "intermediate layer" usually present in *Pachydictyon Binghamiae* is never found, the proper disposition of *D. flabellata* in the genus *Dictyota* in the sense of J. Agardh (1894) and its distinction from *Pachydictyon Binghamiae*, may be assured.

Reexamination of the type and co-type specimens of *Dictyota hesperia* Setchell & Gardner, kindly loaned by the California Academy of Sciences and the University of California, respectively, has revealed that this is not a distinct species and that the original material was incorrectly described.

Sexual reproduction described as "antheridia and oogonia distributed over both surfaces of the same frond, oogonia single and antheridia in small circular groups" is entirely erroneous. A careful check through all of the original material, consisting of some two dozen plants, revealed one oogonial plant and one antheridial plant among many tetrasporic ones. The oogonia proved to be in hemispherical groups of 20–30 as in *Dictyota flabellata*. The antheridia, borne on special plants, are in closely spaced elliptical sori, also as in *D. flabellata*. The description of "oospores germinating freely in position" is incorrect likewise, for the plants of the type collection bearing leaflets are ones heavily parasitized by an endophytic blue-green alga and are not oogonial. Abortive cortical cells of these parasitized plants were evidently mistaken for oogonia, and pustular eruptions of the cortex filled with masses of cells of the unicellular blue-green alga were no doubt mistaken for antheridia. In other collections of *D. flabellata* from the Gulf of California, a number of plants show abundant surface proliferations, but these occur on tetrasporic plants and are independent of the sporangia. Such proliferations have also been observed in *D. flabellata* from southern California, although with less frequency than in the Gulf plants.

Although *Dictyota flabellata* is a common species in southern California, it seems to reach its northern limit somewhere near Santa Barbara. It ranges with *Pachydictyon Binghamiae* down the west coast of Baja California and is the most abundant intertidal *Dictyota* in the northern Gulf of California. Taylor (1945) has reported this species from Costa Rica and from Panama, though his specimens may more probably be referable to the species discussed below, as may also his Panama material identified as *D. Binghamiae*.

DICTYOTA DICHOTOMA (Hudson) Lamouroux. *Dictyota Vivesii* Howe 1911, p. 497; Dawson 1944, p. 229; Taylor 1945, p. 89.

When Howe described his *Dictyota Vivesii* there had been reported from the Pacific Coast of North America only three species of the *Dictyota* assemblage, and the introduction of a fourth from little-known Mexico did not then appear without justification. Collections in recent years, however, have yielded numerous specimens from the Gulf of California, requiring for their interpretation an understanding of *D. Vivesii*. Until the spring of 1949 no fully developed material had been forthcoming from the type locality of Howe's plant, known only to be in the vicinity of La Paz, but at this time a collection was taken in San Lorenzo channel between Isla Espiritu Santo and the mainland of Baja California immediately adjacent to Bahia La Paz. Here were found several of the species originally reported by Howe including what may now be considered topotype material of his *Dictyota Vivesii*. The *Dictyota* specimens are ample and show a considerable range of variation, indicating that the original concept of *D. Vivesii* was

too narrow. Some of the specimens, with entire margins and moderately broad, divaricately branched blades are clearly like Howe's illustration of the type, while other examples are more or less proliferous, with narrowed and less widely spreading segments. An examination of the entire series, together with other similar material from the Gulf of California, suggests strongly the identity of these plants with the widespread and variable *Dictyota dichotoma*. Although the world-wide distribution in warmer waters and great diversity of form recognized by phycologists under the name *D. dichotoma* are not entirely understood, there seems no justification at this time for accepting *D. Vivesii* as distinct from this assemblage.

A further complication arises from the similarity of some phases of *Dictyota flabellata* to some members of the *D. dichotoma* complex, particularly in the Gulf of California where their ranges appear to overlap. On the Pacific Coast of Baja California and in southern California *D. flabellata* is distinctive and sufficiently uniform in its characters that few collections appear which are difficult to recognize. In the Gulf of California, however, the apparently mixed occurrence of *D. flabellata* and *D. dichotoma* makes some immature or atypical examples of each virtually indeterminable. Lacking, with our present knowledge, adequate criteria for distinguishing them positively, we must often resort to probable identifications based on combinations of characters known to be of usual occurrence in each species.

A comparison of Pacific American with Japanese materials within this species-complex seems to indicate that our *D. flabellata* is most like the plant known in Japan as "typical" *D. dichotoma,* whereas the plants herein recognized as *D. dichotoma* agree with other Japanese forms of that species. Atlantic specimens of *D. dichotoma* are seldom to be confused with well-developed *D. flabellata*. It is interesting to note, however, that specimens dredged from Pacific Panama and Costa Rica and determined by Taylor (1945) as *D. flabellata,* seem very much like plants he identified as *D. dichotoma* in the Caribbean (1942). Clearly there remains much to be learned of the distribution of *D. dichotoma,* and the identities of many plants referred to this name must still be considered unsettled.

Compared to the general prevalence of *D. flabellata* in the Gulf of California, particularly in the north, *D. dichotoma* is of infrequent occurrence. Specimens which seem more or less clearly identifiable with the latter are at hand from the following localities: *Dawson 6913,* dredged, San Lorenzo Channel, Baja Calif., Mar. 1949; *Dawson 7071,* dredged, Punta Frailes, Baja Calif., Mar. 1949; *Dawson 3509,* Bahia de San Francisco, Sonora, Nov. 1946; *Dawson 40–155,* dredged off south shore of Isla Tiburon, Sonora, Jan. 1940; *Poindexter,* Punta Peñasca, Sonora, Mar. 1941; *Dawson 1326,* Bahia de Los Angeles, Baja Calif., April 1946. The last two collections represent a small, narrow form.

DICTYOTA DIVARICATA Lamouroux. Taylor 1945, p. 90.

Several new distribution records may be cited for this widespread species of tropical waters which was first recognized in the Pacific Mexican flora by W. R. Taylor from collections taken at Bahia Tenacatita, Jalisco and at Isla Socorro. All of the present specimens show, at least in some parts, the extremely reduced, filiform ultimate segments characteristic of this species.

Hubbs 46–144, Isla Guadalupe, Baja Calif., Dec. 1946; *Dawson 3279*, Punta Palmilla, Baja Calif., Nov. 1946; *Dawson 3086, 3146*, near Punta Frailes, Baja Calif., Nov. 1946; *Dawson 3845, 3895*, Acapulco, Guerrero, Feb. 1947.

DICTYOTA MASONII Setchell & Gardner 1930, p. 148.

Since this seemingly distinctive species has not again been collected since its discovery at Isla Clarion a quarter century ago, no further information can be given concerning it.

DICTYOTA CONCRESCENS Taylor 1945, p. 89.

This species was described from immature, sterile material and by characters too vague for clear interpretation. The type, moreover, is very similar in aspect to another collection from the same station which Taylor has identified as *Dictyota Vivesii*. These collections from Punta Hughes, Baja California leave much to be desired, and it seems at this time impossible to do more than to lay aside the type of *D. concrescens* as an uninterpretable plant until collections can again be made in the type locality at a season when more fully mature material can be secured. It would appear that the months between May and August would be favorable for obtaining such collections.

SUMMARY

The Pacific North American species of Dictyotaceae heretofore known under the name *Dictyota* in the older, broader sense are examined. The generic segregates *Dilophus, Pachydictyon* and *Dictyota* are recognized according to J. G. Agardh, 1894. *Dilophus pinnatus* Dawson is described as new from Nayarit, Mexico. *Pachydictyon Binghamiae* Dawson is a new combination being inclusive of the plants known from Pacific America as *Dictyota Binghamiae* J. Ag., from the Gulf of California as *D. Johnstonii* S. & G. and from Japan as *Pachydictyon coriaceum* (Holmes) Okam. *Dilophus Okamurai* Dawson is a new name for a plant of Japan heretofore known as *Dilophus marginatus* (non J. Ag.) Okam. It is newly reported from Pacific Mexico. *Dictyota cribrosa* S. & G. is recognized as including those plants of the Monterey, California and Cape Arago, Oregon regions heretofore known as *Dictyota flabellata. Dictyota hesperia* S. & G. is shown to have been erroneously described and is reduced under *D. flabellata* (Collins) S. & G. Its distinction from *Pachydictyon Binghamiae* (*Dictyota Johnstonii*) in the Gulf of California is clarified. *Dictyota Vivesii* Howe is reduced under *D. dichotoma* (Huds.) Lamour which is newly reported

from Pacific Mexico. *Dictyota concrescens* Taylor is treated as an inadequately known species.

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SOME FURTHER STUDIES OF INCOMPATIBILITIES IN PETUNIA AXILLARIS[1]

SELMA KOJAN

INTRODUCTION

Incompatibilities are selective physiological reactions which operate to prevent or limit both self and cross reproduction within a single species, and thus compel intergenotypic reproduction within the species.

The literature covering the genetics of intraspecific incompatibilities has been reviewed and critically analyzed by Stout (1938, 1945), and the view expressed that the mechanism of incompatibilities is superimposed on the more fundamental mechanism of reproduction in a species. Hence, the special factors for incompatibility have epistatic relations rather than direct dominance and recessiveness over the basic intraspecific reproduction (Stout 1938).

The oppositional theory of allelic incompatibility factors was first proposed by Prell in 1921 for both self and cross incompatibility in homomorphic flowering plants, and he designated these multiple oppositional factors as O_1O_2, O_1O_3, O_1O_4, etc. He recognized that pollination in most flowering plants involves a relationship between "2n" tissues of the pistil and "n" pollen tubes and that self and cross incompatibilities are antagonistic reactions between a single factor, O_1 or O_2 in a haploid pollen tube and the same factor in the diploid tissues of the pistil. He emphasized that among self-incompatible and completely cross-incompatible diploid individuals of a species, there are two oppositional factors in each individual, e.g. O_1 and O_2, which inhibit growth of pollen possessing one of these factors. Eggs from an individual of genotype O_1O_2 can be fertilized only by male nuclei having neither of these factors. These incompatibility factors are now generally designated as "S" and the particular incompatibility factors as S_1, S_2, S_3, etc. This representation does not include the factors for intraspecific reproduction. These factors may be omitted as long as the plants are hermaphroditic and homozygous for sexuality.

On the basis of the number and behavior of the "S" factors involved, several types of incompatibility have been recognized. The personate type is the simplest type of intraspecific incompatibility and was applied by

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Correns (1928) to intraspecific incompatibility in *Linaria vulgaris* which is now known to be more complex. The personate type involves a relationship between "n" pollen tubes and "2n" tissues of the pistils, and is determined in each individual by a single pair of "S" factors that are also alleles. In these plants the simplest personate type is that in which the "S" factors form one allelic series only, and the factors which affect reproduction are not allelic to the "S" factors. For reproduction in plants which have this type, there must be at least three factors, e.g. S_1, S_2, and S_3 that are combined to give three cross-fertile genotypes in a succession of generations, $S_{1\cdot2}$, $S_{1\cdot3}$, and $S_{2\cdot3}$. Thus, according to the personate type: a. each diploid individual in a species is normally self-incompatible and heterozygous for the special "S" factors; b. individuals having the same "S" factors are cross-incompatible since "n" pollen tubes fail to function in pistils having the same "S" factor; c. any member of one genotype is cross-fertile with any other member of any other genotype, for there is a difference in one "S" factor, and d. when the two individuals have one "S" factor in common, there is hidden incompatibility for the common "S" factor, and the progeny is composed of two genotypes only. In such reactions, there is maximum production of seed, but there is an elimination in the progeny of the genotype of the seed parent and the appearance of a genotype different from either parent. These genotypes can only be demonstrated by the complete analysis of progenies by testing the reactions with each other, with parents, and with known genotypes. For most complete tests, plants which are homozygous for each of the several "S" factors that are involved are of special value for use as testers. Such homozygous plants usually do not occur, but may be obtained by premature pollination. Hidden incompatibility is illustrated in the cross $S_{1\cdot2} \times S_{2\cdot3}$, in which $S_{1\cdot2}$ is the seed parent, and can be discovered and demonstrated when the progeny is properly analyzed. The S_2 factor is common to both pistil and pollen, hence pollen tubes carrying this factor fail to function in the styles of the pistil. Pollen tubes carrying the S_3 factor do not encounter that same factor in the pistils, and consequently, they are the only ones which are able to function in the styles and reach the ovules. Male nuclei carrying this S_3 factor unite with the egg nuclei carrying the S_1 or S_2 factor. Therefore, the two mating groups represented in the progeny are $S_{1\cdot3}$ and $S_{2\cdot3}$. The genotype of the seed parent, $S_{1\cdot2}$, does not appear in the progeny; neither does the genotype, $S_{2\cdot2}$ appear. But there is a new genotype, different from the genotype of either parent, that appears in the progeny, $S_{1\cdot3}$.

When two individuals have no "S" factor in common, there is no hidden incompatibility and both classes of pollen are able to function and therefore four mating groups should appear in the progeny, but the geno-

type of both the seed and pollen parents are selectively eliminated in the offspring. An example of a cross in which there is no hidden incompatibility is $S_{1\cdot2} \times S_{3\cdot4}$. The seed and pollen parents have no common "S" factor, and therefore, both classes of pollen are able to function in the styles of the pistils. Four mating groups should appear in the progeny: $S_{1\cdot3}$, $S_{2\cdot3}$, $S_{1\cdot4}$, and $S_{2\cdot4}$,—the genotypes of both the seed and pollen parents have been eliminated in the progeny. Thus, when two parents have no incompatibility factor in common, both classes of pollen tubes function, and neither of the parental genotypes appear in the offspring.

The genetics of the personate type of incompatibility is fairly well known, and there is evidence to show that the various "S" factors exhibit different degrees of reactions (Stout 1938, 1945). The biochemical nature of these inhibitory substances, however, has not been determined, but it has been suggested (Stout 1916) that incompatibilities may be antigen—antibody reactions. This interpretation has recently been applied by Lewis (1943).

Diploid plants of many species, eg. *Petunia axillaris*, normally do not set seed to self-pollination, but when close pollinations are made in the bud before the secretion has developed on the stigma, incompatibility reactions are not complete. This method, which was employed by East, consists of taking fresh pollen from a dehisced anther of one flower and placing it on an immature stigma of another flower still in the bud stage. In this way, some pollen tubes are able to function in styles of pistils having the same "S" factor. When seeds from these premature pollinations are grown, three genotypes usually occur in the progeny, e.g. $S_{1\cdot3}$ selfed prematurely gives $S_{1\cdot3}$, $S_{1\cdot1}$, and $S_{3\cdot3}$ genotypes in the progeny. Similar results have been reported in other plants, eg. in cabbage (*Brassica oleracea*) when controlled bud pollinations of self-incompatible plants were made.

An excellent review of the cytological phenomena connected with self-sterility in the flowering plants is given by Sears (1937). In some cases incompatibility reactions occur on the surface of the stigma. Studies in a number of plants indicate that inhibitory substances may be produced in the papillae of the stigma (Jost 1907, Stout 1931, Riley 1934, 1936). In many cases, incompatibility reactions occur in the style (Jost 1907, Stout 1931, 1938, East 1934). Other cases show that these inhibitory substances may be located in the ovary or even in the ovule (Stout 1931, Stout & Chandler 1933, Yasuda 1933, 1934). Thus, these inhibitory substances may inhibit pollen tube growth in the stigmatic region, in the style, or even in the ovary. Conspicuous coiling of many pollen tubes on the surface of the papillae of the stigmas, in stylar tissues, on walls of the placentae, in the micropylar regions, and within the ovules in the immediate vicinity of the embryo sac or in contact with it, were observed in *Brassica pekinensis*

during the period in which the plants showed self-incompatibility (Stout 1931).

Problem. This study is a continuation of investigations of incompatibility in diploid members of *Petunia axillaris* (Lam.) B.S.P. (P. nyctaginiflora, Juss.) initiated by Dr. Stout of the New York Botanical Garden. Plants homozygous for $S_{1\cdot1}$ and $S_{3\cdot3}$ were obtained. The identity of such plants is revealed by their own reactions and by the progeny which they give when prematurely selfed or crossed with known genotypes. A plant belonging to genotype group $S_{3\cdot3}$ was analyzed and two pedigreed progenies involving the homozygous genotype $S_{3\cdot3}$ as the seed parent, and heterozygous genotypes as the pollen parents, were grown and analyzed to test whether hidden incompatibility was complete. In these progenies, as in all progenies of diploid *Petunia axillaris*, the personate type of incompatibility is involved.

This problem is concerned with the evaluation of the genetic constitution and reactions of a plant of diploid *Petunia axillaris* of the genotype group $S_{3\cdot3}$ that was obtained from the premature pollination of a plant of genotype $S_{2\cdot3}$. To complete the evaluation, a typical plant of this genotype $S_{3\cdot3}$ was crossed as a seed parent with known plants of $S_{2\cdot3}$ and $S_{1\cdot3}$, and each of the two progenies was fully analyzed to help determine whether hidden incompatibility was complete. Since in hidden incompatibility, a full complement of seed is obtained, there is no indication of incompatibility in the immediate resultant. Hence, hidden incompatibility can only be determined fully through experimentation by: 1. knowing the genotypes of both the seed and pollen parents of a particular cross and then growing the progeny; 2. analyzing the progeny and determining their reactions with each other and as seed and pollen members with both parents, thus demonstrating the genotype of all the seedlings and giving further proof of the genotypes of both parents; 3. obtaining all of the possible progenies for all genotypes involved, e.g. when the "S" factors S_1, S_2, and S_3 factors are involved, progenies involving all possible genotype combinations of these three factors should be grown and analyzed: Several different genotype crosses of the diploid genotypes $S_{1\cdot2}$, $S_{1\cdot3}$, and $S_{2\cdot3}$ can be made and the progenies grown and analyzed, $S_{1\cdot2} \times S_{1\cdot3}$, $S_{1\cdot3} \times S_{1\cdot2}$, $S_{1\cdot2} \times S_{2\cdot3}$, and $S_{3\cdot3} \times S_{1\cdot3}$. In addition, all possible progenies involving the homozygous genotypes must be grown and analyzed, e.g. $S_{1\cdot1} \times S_{1\cdot3}$, $S_{3\cdot3} \times S_{2\cdot3}$, etc.

The two progenies that were grown and analyzed were:

I. 268-9[2] ($S_{3\cdot3}$) × 268-3[3] ($S_{2\cdot3}$) Series 403

II. 268-9 ($S_{3\cdot3}$) × 295-16 ($S_{1\cdot3}$) Series 404

[2] The number 268 refers to a seed planting from a single capsule of a particular pedigree. Number 9 refers to a particular seedling from a seed of that capsule.

[3] The parent to the right of the "X" sign is the pollen parent.

The parent plants of the two progenies were of material previously studied and pedigreed, and the "S" factors of the parents and tester genotypes had been identified and designated as S_1, S_2, S_3, S_4, S_5, S_6.

The genotypes had already been fully determined for all combinations of S_1, S_2 and S_3, and for $S_{3\cdot3}$ and $S_{1\cdot1}$, but not for the progenies of $S_{3\cdot3}$ and $S_{2\cdot3}$ or $S_{3\cdot3}$ and $S_{1\cdot3}$.

Methods. In January, 1948, plants of known genotypes of 2n *Petunia axillaris* and capsules of seeds of known pedigrees were obtained from Stout. The diploid plants represented seven genotypes previously identified and kept in clonal propagation to be used as testers for seedling progenies and included $S_{1\cdot1}$, $S_{3\cdot3}$, $S_{1\cdot2}$, $S_{1\cdot3}$, $S_{4\cdot5}$, and $S_{5\cdot6}$. The capsules of seeds represented the following progenies: $S_{3\cdot3} \times S_{2\cdot3}$, and $S_{3\cdot3} \times S_{1\cdot3}$.

The two groups of seedlings were assigned series numbers 403 and 404, and the seeds from each capsule were sown in a separate seed pan in the greenhouse. Seedlings from each series were grown and assigned numbers 1–35 as soon as they were taken from the seed pans and potted in individual pots. When these seedlings were in full bloom during the summer of 1948, controlled pollinations were made to test each seedling in self and in reciprocal cross-pollinations with other seedlings of the same series. Since it was necessary to find out which incompatibility factors were present in the seedlings, each seedling was crossed both as seed and as pollen members with known genotypes as testers. The pollination results were uniform for series 403 and 404, and the results from twenty-five seedlings each were selected in making charts I and II.

Results. I. 268-9 ($S_{3\cdot3}$) $\times$ 268-3 ($S_{2\cdot3}$) Series 403.

Chart I shows the pollination results for this series. Each of the twenty-five seedlings was self-incompatible (S) because each class of pollen encountered its own factor in the 2n pistil. All of the members of this series were intra-cross-incompatible (O). These results indicate that all of the seedlings of series 403 were of the same genotype.

Since the seed parent of series 403 was genotype $S_{3\cdot3}$, and the genotype of the pollen parent was $S_{2\cdot3}$, it was most important to test for these factors in the progeny. As shown in Chart I, all the seedlings were cross-incompatible as seed members with pollen from $S_{3\cdot3}$ testers. This showed that the seedlings had the S_3 factor. All the seedlings were cross-incompatible with pollen of $S_{2\cdot3}$ testers. When the seedlings were backcrossed on $S_{2\cdot3}$ testers as seed members, every result was likewise "O". Therefore, all the seedlings were genotype $S_{2\cdot3}$ which is the same genotype as their pollen parent. This status was verified further by results of the tests of the progeny as pollen members on other testers. The relations were fully incompatible only on $S_{2\cdot3}$ seed parents. Thus, in the relations of the parents $S_{3\cdot3} \times S_{2\cdot3}$, no S_3 pollen tubes had functioned; on only S_2 pollen had func-

tioned. The ovules were functional since good-sized capsules with many seeds were obtained when these seedlings were used as seed members with pollen of $S_{1\cdot1}$, $S_{1\cdot3}$, $S_{1\cdot2}$, $S_{5\cdot6}$ genotypes, as is shown in Chart I.

II. 268-9 ($S_{3\cdot3}$) × 295-16 ($S_{1\cdot3}$) Series 404

Chart II shows the pollination results for series 404. Here again, it is apparent that all of the seedlings of this series were not only self-incompatible, but also cross-incompatible with each other. The seedlings were also reciprocally incompatible in crosses with $S_{1\cdot3}$ testers. These results indicate that only pollen tubes that carried the S_1 factor had functioned in the $S_{3\cdot3}$ pistil. When these seedlings were used as seed members in crosses with genotypes $S_{1\cdot1}$ and $S_{3\cdot3}$, as pollen members, the results were always "O". This verified the previous results that they were of genotype $S_{1\cdot3}$. But when the pollen of these seedlings was placed on all of the other tester genotypes, except $S_{1\cdot3}$, capsules with many seeds were produced every time. These results of tests demonstrated that the seedlings had the S_1 and S_3

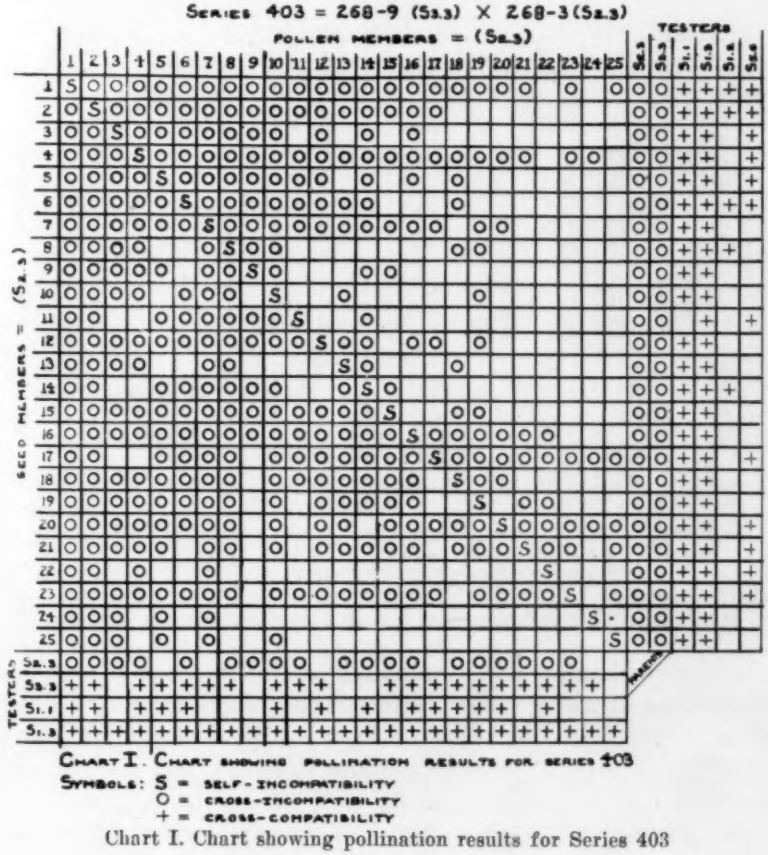

Chart I. Chart showing pollination results for Series 403

factors only. The ovules of these seedlings were functional since every cross that was made with pollen of genotypes $S_{1\cdot2}$ and $S_{2\cdot3}$ resulted in good-sized capsules containing many seeds.

SUMMARY

1. This research is concerned with the evaluation of the constitution of a plant of the genotype group $S_{3\cdot3}$ which had the reactions characteristic of, and expected of, plants that were $S_{3\cdot3}$.

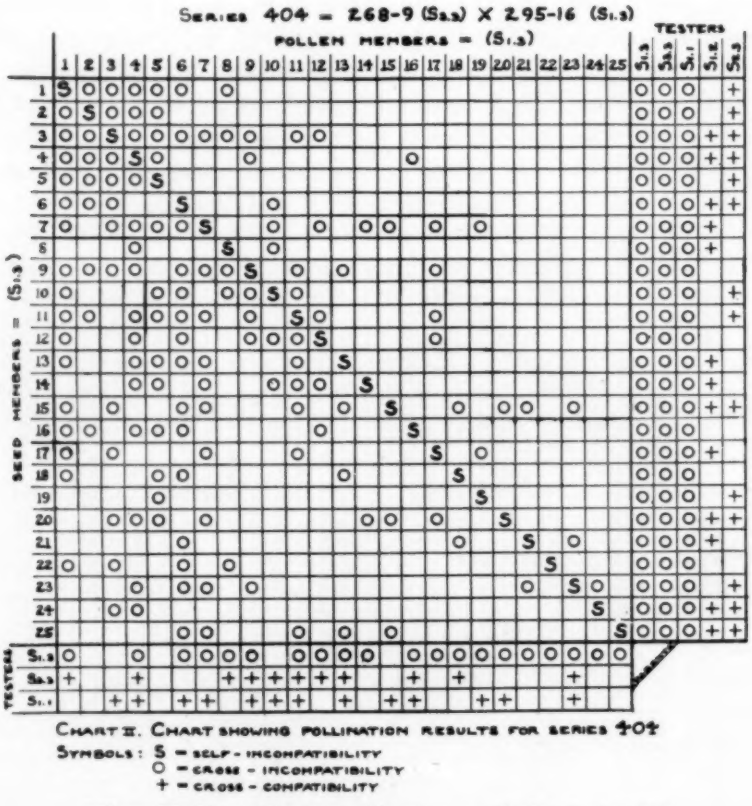
SERIES 404 = 268-9 (S3.3) × 295-16 (S1.3)
POLLEN MEMBERS = (S1.3)
TESTERS
SEED MEMBERS = (S1.3)
TESTERS
CHART II. CHART SHOWING POLLINATION RESULTS FOR SERIES 404
SYMBOLS: S = SELF-INCOMPATIBILITY
O = CROSS-INCOMPATIBILITY
+ = CROSS-COMPATIBILITY

Chart II. Chart showing pollination results for Series 404

2. In order to complete the evaluation, a typical plant of the genotype $S_{3\cdot3}$ was crossed as a seed parent with known plants of genotypes $S_{1\cdot3}$ and $S_{2\cdot3}$ as pollen members. Two such pedigreed progenies: 268-9 $(S_{3\cdot3}) \times (S_{2\cdot3})$ and 268-9 $(S_{3\cdot3}) \times (S_{1\cdot3})$ were grown and analyzed, and the results fully demonstrated that the genotype of the seed parent was $S_{3\cdot3}$.

3. The progeny of $S_{3\cdot3} \times S_{2\cdot3}$ (Series 403) was composed of one genotype

whose reactions were characteristic of $S_{2\cdot3}$. Hence, plant 268-9 was $S_{3\cdot3}$, and in the reactions of the cross, only pollen tubes that were S_2 had functioned.

4. The progeny of $S_{3\cdot3} \times S_{1\cdot3}$ (Series 404) was composed of one genotype whose members had the reactions characteristic of $S_{1\cdot3}$. Hence, the plant 268-9 was $S_{3\cdot3}$, and in the reactions of the cross, only pollen tubes that were S_1 had functioned.

5. The two test progenies collectively involved the hidden incompatibility of S_3 pollen tubes and the functioning of S_1 and S_2 pollen tubes, and were hence complete for the reactions of the factors S_1, S_2, and S_3, in the evaluation of the $S_{3\cdot3}$ genotype.

6. The reactions which showed that all the original plants obtained by premature self-pollination of a plant that was genotype $S_{2\cdot3}$, were of genotype $S_{3\cdot3}$ are:

a. As pollen members, plants of $S_{3\cdot3}$ were fully incompatible with $S_{1\cdot3}$.

b. As seed members, they were cross-fertile with $S_{1\cdot3}$ and $S_{2\cdot3}$.

c. Members of the genotype group $S_{3\cdot3}$ were intra-incompatible.

The progeny analysis which showed that these plants were $S_{3\cdot3}$ are:

d. As seed parents with $S_{2\cdot3}$, the progeny was composed of one genotype, $S_{2\cdot3}$.

e. As seed parents with $S_{1\cdot3}$, the progeny was composed of one genotype, $S_{1\cdot3}$.

7. Plant 268-9 was a typical plant of the entire progeny obtained by premature self-pollination of a plant that was $S_{2\cdot3}$. All these seedlings had the same reactions. The progeny tests of plant 268-9 prove that its genetic constitution was $S_{3\cdot3}$. Presumably, all of its sister seedlings were also $S_{3\cdot3}$.

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THE METABOLISM OF CARBOHYDRATES BY NEUROSPORA

D. PERLMAN

During the past eight years a considerable number of reports have appeared describing investigations of nutritional requirements of mutant strains of *Neurospora*. Many of these studies have been concerned with the mechanisms of the biosynthesis of vitamins and growth factors and have elaborated the approach to this problem suggested by the observations of Prof. G. W. Beadle and his associates (1941; 1945a; 1945b; Ryan *et al.*, 1943; Mitchell *et al.*, 1946). The mutant cultures have been grown on a basal synthetic medium containing carbohydrate, inorganic salts, biotin, and supplemented with vitamins and growth factors in most of these studies. This medium was derived from that used by Fries (1938) who used sucrose as carbohydrate source. Stokes *et al.* (1943) observed that glucose, maltose, xylose, and perhaps raffinose could probably be substituted for the sucrose without marked effect on mycelial growth. They also noted that the "pyridoxinless" culture of *Neurospora sitophila* they were studying would not grow on synthetic media in which lactose, inulin, or mannitol was used as a replacement for the glucose and concluded that the fungus was unable to utilize these carbohydrates. Hodson (1945) also noted that the fungus was unable to grow on media containing lactose.

Apparently the interest of these investigators has centered mainly around mechanisms of synthesis of vitamins and growth factors by these organisms, and these reports indicate that little attention has been paid to the carbohydrate metabolism of these fungi. Lewis (1948) has suggested that these organisms metabolize carbohydrate through a similar mechanism as found in yeasts as indicated by his studies with mutants requiring succinic acid. The following experiments and others to be reported elsewhere (Perlman, 1950) indicate that the normal products of carbohydrate metabolism by these fungi include carbon dioxide, acetic acid, ethanol, and oxalic acid when the cultures are grown on synthetic media in surface or submerged culture.

As mentioned above, biotin is apparently the only growth factor required by these normal cultures (Butler *et al.*, 1941). Recent studies with bacteria and animal tissues have suggested that this vitamin is involved as a coenzyme in the dissimilation of intermediates of carbohydrate fermentation. A few analogues of biotin have been tested for biotin-like activity (Lilly and Leonian, 1944; Tatum, 1945) and several experiments have been completed studying possible differences in carbohydrate metabolism which

might occur when these analogues were substituted for biotin in the synthetic medium.

Methods. Seven cultures of *Neurospora* were used in these experiments including *Neurospora sitophila* and *Neurospora crassa* (wild types) and five mutants which required respectively uracil, leucine, lysine, tryptophane, and pantothenic acid for growth. These cultures were grown on the basal medium (supplemented in the case of the mutants with the appropriate substances) containing agar (1.5%) and transferred at approximately bi-monthly intervals. The basal medium contained (g./1.) : glucose (or other carbohydrate as indicated), 10 g.; *dl*-biotin, 20 μg.; Zn (as $ZnSO_4 \cdot 7H_2O$), 1 mg.; Fe (as $Fe\ SO_4 \cdot 7H_2O$), 1 mg.; Ca (as $CaCl_2$), 1 mg.; $MgSO_4 \cdot 7H_2O$, 0.5 g.; KH_2PO_4, 1.5 g.; $NH_4H_2PO_4$, 3 g.; distilled water to 1 liter; pH adjusted with KOH to 7 before use. When the mutant cultures were studied this medium was supplemented with 0.1 mg per liter of the appropriate substance. The carbohydrates used for replacements for the glucose were obtained from Merck and Co., Inc. (maltose, sucrose, dextrin, lactose, galactose, sorbose, starch), Eastman Kodak (sorbitol, mannitol), and the Difco Co. (fructose, inulin, xylose). The biotin and biotin analogues were obtained from the Hoffman-La Roche Laboratories and were synthetic products.

The cultural techniques used were similar to those used in previous studies (Perlman, 1948; 1949; 1950). When surface culture conditions are mentioned the organisms were grown in cotton plugged 125 ml Erlenmeyer flasks containing 40 ml of medium. The flasks were inoculated (after sterilization by autoclaving at 121° C. for 15 min.) with a homogenized cell suspension obtained by homogenizing a 5 day old mycelial pad in a Waring blender. A number of replicate flasks were arranged (usually 4) and two were harvested at the end of the indicated incubation interval, the mycelial growth removed for analysis, and the contents pooled before analysis. The cultures were incubated in a room whose temperature varied between 25° and 28°. The submerged culture experiments were conducted with the apparatus used in previous studies with *Polyporus anceps* (Perlman, 1949). Humidified sterile air was passed through the fermentation flasks (placed on the rotary shaker) at a rate of 80 ml per hour.

The analytical methods used were those used in previous studies (Perlman, 1945: 1948) for the determination of ethanol, acetic acid, oxalic acid, total carbon in solution, carbon dioxide, and mycelium weight.

Experimental and Discussion. The culture of *N. crassa* (wild type) was grown in surface culture on the basal medium with a number of carbohydrates replacing glucose. Fermentation flasks were removed after 3 and 6 days incubation and analyzed with results as summarized in table 1 (A). Negligible growth was obtained when the glucose was replaced by lactose,

TABLE 1. *Metabolism of Carbohydrates by Neurospora crassa*

A. Surface Culture

Carbohydrate	0 day		3 days incubation							6 days incubation					
	pH	carbohydrate	pH	carbohydrate	ethanol formed	acetic acid	oxalic acid	carbon in sol'n.	mycelium weight	pH	carbohydrate	ethanol formed	acetic acid	oxalic acid	mycelium weight
		mg/ml		mg/ml	mg/ml	mg/ml	mg/ml	mg/ml	mg/ml		mg/ml	mg/ml	mg/ml	mg/ml	mg/ml
glucose	6.8	9.7	5.3	3.7	0.6	0.4	0.1	2.1	2.3	4.3	1.1	0.5	0.4	0.3	3.5
maltose	7.1	9.8*	4.7	4.9*	1.0	0.5	0.1	2.3	2.6	4.3	0.6*	0.8	0.6	0.2	2.7
dextrin	6.8	8.9*	4.8	3.7*	1.0	0.3	0.2	1.7	2.8	4.5	0.5*	0.6	0.5	0.3	3.9
starch	6.9	8.9*	4.9	4.1*	1.1	0.3	0.2	1.9	3.1	4.7	0.5*	0.7	0.4	0.2	4.6
mannitol	6.9		6.8					4.0	negligible	6.6					negligible
sorbitol	6.9		6.8					3.8	negligible	6.3					negligible
sorbose	6.9	9.8	6.8	9.3				3.6	negligible	6.4	9.1				negligible
fructose	6.5	9.9	4.7	3.6	0.9	0.4	0.1	2.1	2.0	4.6	0.8	0.6	0.3	0.3	3.6
sucrose	7.3	9.8*	5.0	4.9*	0.6	0.4	0.1	1.9	1.8	4.1	0.5*	0.1	0.5	0.2	3.7
inulin	7.1	9.5*	5.3	4.1*	0.5	0.3	0.2	2.9	2.3	4.3	0.4*	0.2	0.3	0.2	3.9
galactose	7.3	8.9	4.9	5.0	0.4	0.4	0.1	3.1	1.6	4.6	0.6	0.3	0.4	0.2	2.8
lactose	7.1	9.6*	6.8	9.3*				4.3	negligible	6.3	9.0*				negligible
xylose	7.0	9.5	4.9	4.6	0.6	0.2	0.2	2.9	1.4	4.8	0.8	0.3	0.3	0.3	2.3

* After hydrolysis.

TABLE 1—(*Continued*)

B. Submerged Culture

	0 day		3 days incubation							
Carbohydrate	pH	carbohydrate	pH	carbohydrate	carbon dioxide formed	ethanol formed	acetic acid formed	oxalic acid formed	carbon in sol'n.	mycelium weight
		mg/ml		mg/ml	mg/ml	mg/ml	mg/ml	mg/ml	mg/ml	mg/ml
glucose	6.8	8.9	4.3	1.0	5.8	2.3	0.3	0.3	1.6	3.6
maltose	6.9	9.3*	4.1	0.8*	6.1	1.9	0.6	0.4	1.7	4.6
dextrin	7.0	9.5*	4.5	1.9*	5.8	2.6	0.6	0.3	1.6	4.3
starch	6.9	9.3*	4.7	0.8*	5.7	1.6	1.0	0.6	1.3	4.3
fructose	6.5	9.1	4.6	1.0	6.3	0.9	0.7	0.4	0.7	3.1
sucrose	6.9	10.0*	4.5	0.8*	6.5	2.7	0.6	0.3	1.9	3.9
inulin	6.7	9.8*	4.7	0.3*	6.1	1.6	0.6	0.3	1.6	3.6
galactose	6.9	9.0	5.1	0.9	6.3	2.7	0.6	0.1	2.0	3.7
xylose	6.5	9.4	4.9	0.6	6.3	1.6	0.3	0.1	1.6	2.1

* After hydrolysis.

sorbitol, mannitol, or sorbose as previously noted by Stokes *et al.* (1943) while good growth was obtained when inulin was substituted. This latter observation is not in agreement with that of Stokes *et al.* and may perhaps be explained on the basis that the inulin used in the experiment in table 1 was contaminated with fructose. However, reasoning from the observations with glucose and starch, it seems likely that good growth should be expected when inulin is used as fructose is a satisfactory substrate.

The analysis of the fermented medium indicated that significant quantities of ethanol and acetic acid were present accompanied by smaller amounts of oxalic acid. These three products appear to account for more than 90% of the carbon in solution (after correction for the unutilized carbohydrate has been made). It is assumed that the carbon unaccounted for originally supplied as glucose has been transformed to mycelium or carbon dioxide.

The above experiment was repeated in submerged culture with the corresponding analyses summarized in table 1 (B). The apparatus used permitted an analysis for carbon dioxide formed when submerged culture conditions were used. As indicated in the table, ethanol, carbon dioxide, acetic acid, and oxalic acid apparently account for nearly all of the carbon supplied to the fermentation as carbohydrate. While the organism grows rapidly under submerged culture conditions, the use of the homogenized mycelium as inoculum apparently prevented the formation of the large "ball type" mass which had hampered earlier experiments.

Study of the data accumulated suggests that this organism metabolizes hexoses or polymers of hexoses much the same way it metabolizes pentoses. Whether or not the same enzymatic mechanism operate in the metabolism of hexoses by this organism as are found in yeast is undecided. Other experiments (Perlman, 1950) as well as these indicate that the organism will

TABLE 2. *Metabolism of Glucose by Neurospora cultures in Surface Culture*

Culture	0 day	5 days incubation				
	pH	pH	glucose*	ethanol	acetate	oxalate	mycelium
			mg/ml	mg/ml	mg/ml	mg/ml	mg/ml
Neurospora crassa (wild type)	6.9	4.6	8.8	1.3	0.2	0.1	3.9
uracilless	6.9	4.3	8.3	1.6	0.5	0.3	3.8
lysineless	6.9	4.7	6.9	1.4	0.3	0.1	3.6
leucineless	6.9	4.4	7.8	1.7	0.3	0.2	3.6
tryptophaneless	6.9	4.9	7.9	1.8	0.3	0.2	3.1
N. sitophila	6.9	4.5	8.3	1.6	0.3	0.1	3.6
pantothenicacid less	6.9	4.6	8.3	1.3	0.4	0.1	3.5

* Glucose utilized; original concentration before inoculation: 9.3 mg/ml.

metabolize ethanol, and suggest that the acetic acid is formed by the metabolism of the ethanol present.

Approximately the same quantities of metabolic products were formed from glucose by the mutant cultures as by the wild type as indicated in table 2. This suggests that the treatment producing these mutants did not result in significant change in their mechanisms for the metabolism of glucose.

As has been mentioned previously, several reports have been noted in the

TABLE 3. *Biotin and O-heterobiotin as Growth Factors for Neurospora crassa*

Concentration added	*dl*-biotin					*dl*- O-heterobiotin				
	pH	glucose* utilized	ethanol formed	acetic acid	mycelium weight	pH	glucose* utilized	ethanol formed	acetic acid	mycelium weight
ug/l.		mg/ml	mg/ml	mg/ml	mg/ml		mg/ml	mg/ml	mg/ml	mg/ml
0.000	6.8	0.6	0.0	0.0	0.3	6.8	0.9	0.0	0.0	0.2
0.002	5.3	3.8	0.3	0.0	1.0	6.8	0.8	0.0	0.0	0.3
0.006	5.1	7.9	1.1	0.3	1.7	6.8	0.7	0.0	0.0	0.4
0.02	4.6	8.1	1.8	0.3	2.6	6.8	0.9	0.0	0.0	0.4
0.06	4.4	8.3	1.9	0.4	2.9	6.0	0.9	0.0	0.0	0.6
0.2	4.5	8.4	1.9	0.3	2.8	5.1	5.1	0.9	0.2	1.8
0.6	4.3	8.1	1.8	0.4	2.9	4.3	7.9	1.3	0.3	2.3
2.0	4.4	8.0	1.9	0.4	2.7	4.4	8.5	1.5	0.3	2.8

* Original glucose concentration before fermentation: 8.7 mg/ml 5 day fermentation period; surface culture.

literature concerning the biotin requirement of *Neurospora* cultures. The data presented in table 3 indicate that the metabolism of glucose is not markedly changed when biotin is the limiting factor for growth. Apparently the cells formed metabolize glucose at a definite rate, and if more cells are formed, more glucose is metabolized. This would indicate that biotin has its main role in controlling growth. O-heterobiotin may be substituted for biotin, but is apparently only 3% as active as an equal weight of biotin in promoting growth (it is assumed that only the *d* isomer promotes growth, based on evidence found in the literature). However, mixtures (95:5) of O-heterobiotin and biotin were found to be as active as a weight of biotin equal to the total weight of the mixture, suggesting that biotin has a potentiating effect on the utilization of O-heterobiotin. When (synthetic) aspartic acid was added to the medium at a level of 10 mg. per l. the biotin requirement for maximum growth was reduced to appproximately 15% of that required when the aspartic acid was not added, as result similar to that noted when a similar experiment was performed with *Memnoniella echinata* (Perlman, 1948).

Contrary to reports in the literature, (synthetic) desthiobiotin was found to be inactive as a replacement for biotin. In these experiments two samples of desthiobiotin were used, one made by degradation of (synthetic) biotin* and the other by organic synthesis. The material made by degradation was found to have a small amount of biotin present (Dr. J. L. Stokes, personal communication). Mixtures of the inactive (synthetic) desthiobiotin and biotin (95:5 to 30:70) were as active as an equivalent weight of biotin (to the mixture). This may account for the activity of the desthiobiotin made by degradation processes.

The author wishes to express his appreciation to Prof. H. K. Mitchell, Prof. E. F. McCoy, and Prof. H. S. Loring for the cultures used in these experiments. He is also indebted to Dr. Harold B. Woodruff for the use of certain laboratory facilities during some of these experiments.

SUMMARY

Ethanol, acetic acid, oxalic acid, and carbon dioxide apparently account for nearly 95% of the carbon metabolized by cultures of *Neurospora* as carbohydrate when grown in surface or submerged culture on a synthetic medium.

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* Generously supplied by Dr. J. L. Stokes.

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THE GROWTH OF NORMAL PLANT TISSUE IN VITRO AS AFFECTED BY CHEMICAL CARCINOGENS AND PLANT GROWTH SUBSTANCES. III. THE CULTURE OF SUNFLOWER AND TOBACCO STEM SEGMENTS*

MICHAEL LEVINE[1]

Normal plant tissues grown *in vitro* have been studied principally by the French workers, Gautheret (1945) and Nobécourt (1937), and their students. These workers developed techniques for bringing the cambial tissue of trees, such as the willow, elm, sycamore under *in vitro* cultivation, also the shoots of various vines and the fleshly storage organs of the garden variety of plants, the carrot, turnip, Jerusalem artichoke, salsify and endive. Not only were the microscopical changes in the primary inocula investigated, but the outgrowths, the calluses from the initial fragments were cutivated on synthetic media *in vitro* as tissue cultures and their propagation has now extended over a period of years. The production of these tissue cultures on synthetic media thus advanced our knowledge of growth of plant tissues. Animal cells, to be grown *in vitro* first, must still depend entirely for their nourishment on complex organic substances such as plasma, serum, chick embryo extract and adjuvants, such as Tyrode or Locke, or other salt solutions.

In America, White and Braun (1939, 1941, 1942, 1943) and DeRopp (1947, a, b, & c) at the Rockefeller Institute at Princeton, studied pathological plant material *in vitro* almost exclusively. These workers cultivated the atypical proliferation from the tobacco hybrid tumor first described by Kostoff (1935) and later studied by Whitaker (1934). Both workers described these growths as similar to crown galls, an interpretation with which the present writer (1937) is not in accord. The other tissues studied consisted of the bacteria free tumor tissue of the sunflower and the heat-treated tumors of *Vinca rosea* (White 1945). Segments of normal tissues of the sunflower, tobacco, and tomato were grown *in vitro* and studied incidental to the pathological material. These were primary culture studies based entirely on the inoculum and were devised especially to test the reactions of normal tissue to the influence of substances diffused from the crown gall.

The hybrid tobacco callus has been studied by Skoog (1944) in its relation to auxins. Hildebrandt and Riker (1947) studied the effect of growth regulating substances and the effect of different sources of carbon (1949) on

[1] These studies were aided by a grant from the American Cancer Society, Inc. upon the recommendation of the Committee on Growth of the National Research Council.

the growth of bacteria free crown gall tissue of the marigold, Paris daisy, sunflower, periwinkle and apical stem segments of the hybrid tobacco. Riker and Gutsche (1948) used sunflower crown gall tissue material to study the effects of nitrogen from various sources on growth.

Recently Skoog and Cheng Tsui (149) described controlled growth of bud formation of the callus formed from quadrants of stems of *Nicotiana tabacum*. The inhibitory effects of heteroauxin were overcome by the addition of adenine coupled with an increase in the phosphate and sucrose content of the White's medium used. Adenine induces bud formation in both callus and stem internode tissue under the conditions of their experiments.

It seemed of interest to study the behavior of fundamental tissues as derived from segments of stem of the sunflower and tobacco under the influence of nutrient agar in which the chemical carcinogens had been suspended. The effect of the chemical carcinogens, such as 1,2,5,6-dibenzanthracene (D); 3,4-benzpyrene (B) and 20-methylcholanthrene (M) is known to be highly carcinogenic for animals and their application to the surface injuries of plants *in situ* failed to produce malignant growths. It was thought that the fundamental meristematic outgrowths from some plants would be more susceptible to the influence of the carcinogens for these could be supplied in various concentrations and their effect on growth, development and differentiation could be studied.

In the two previous reports on the effects of these hydrocarbons on carrot tissue, it was revealed that dibenzanthracene and methylcholanthrene enhanced growth and differentiation but not too much in excess of the growth on standard medium. The plant growth substance, indole acetic acid, had an inhibitory effect on organ formation but it seemed to prepare the tissue for complete differentiation when the tissue grown on it was removed from its influence and seeded on a medium with one of the carcinogens and the basic mineral nutrient, organic substances and some vitamines.

The histological and cytological studies of these treated carrot tissues revealed bizarre arrangement of lignified elements such as occur in crown gall tissue. This crown gall like tissue appeared after growth on the carcinogens and indole acetic acid. Aberrant histological and cytological behavior was noted in the tissue mass, the thallus-like growths and the fully developed plantlets that appeared in these cultures. Giant cells with well differentiated nuclei appeared in these treated tissues. The nuclear divisions appeared normal and the presence of polyploid nuclei such as occur in crown gall could not be determined (Levine 1934). It was concluded that the carcinogens induce cellular changes not unlike those induced by the inciting organism in the crown gall disease. Further, it was contended that malignancy in the sense that it occurs in animals and man does not occur in plants either through the injection of the plant tumor producing organism or the chemical

carcinogens. The proliferative reaction induced in plants by these and other agents is a protective response. The effect of these chemical carcinogens had been investigated on plants grown *in situ* in the previous decade (Levine 1934, 1936, 1940) and the conclusions reached then have not been altered.

Materials and Methods. Sunflower seedlings, *Helionthus annus* var. Russian grown in the greenhouse or garden, approximately 25 to 30 cm. tall were carefully removed and cut into segments 3 to 5 mm. long after the outer epidermis had been stripped from them. The species of tobacco studied were principally *Nicotiana Langsdorffii, N. affinis* and *N. tabacum*. Growth of the internodal segments of *N. glutinosa* and *N. glauca* was also started and developed in the early stages. Acknowledgment is made to Doctor L. O. Kunkel for his kindness in placing at our disposal the seeds of the tobacco plants used in these experiments. Axillary shoots of the burley variety of tobacco were used while the apical protion of the stems of the other species were selected after growth in the garden. These stems were removed, rinsed quickly in 80 per cent alcohol and after removing the outer epidermis were cut into segments 5 to 7 mm. in height. The diameter of the larger segments of *N. tabacum* was approximately 3 to 5 mm.

The medium compounded by White (Ws) and later those of Hildebrandt, Riker, and Duggar for sunflower (Wsf) and tobacco (Wt) were used. Shredded agar 0.6 to 0.8 per cent, washed in distilled water for 3 to 4 days was added. The chemicals used were of the reagent grade and Abbott's pyrogen-free water was used throughout as solvent. Pyrex glass, cleansed with sodium triphosphate was used exclusively. The addition of traces of heteroauxin, indole acetic acid (IAA) and α-naphthalene acetic acid (NAA) stimulated growth and induced proliferation of callus tissue that could be removed from the inoculum to initiate true tissue cultures.

The new growths that developed after several transplants were divided and planted on media in which the carcinogens 1,2,5,6,-dibenzanthracene (D); 3,4-benzpyrene (B) and 20-methylchollanthrene (M) were incorporated. These chemicals were disolved in double distilled benzene and added to the nutrient medium.

* I. The culture of the carrot taproot meristem. Am. Jour. Bot. 37(—): 1950.
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The agar medium was made up in batches of a liter each, divided into 25 ml. parts and placed in 40,125 ml. Erlenmeyer flasks. These were autoclaved for 20 minutes at the pressure of one atmosphere, during and after which the carcinogens crystallized out and the benzene was driven off. The culture to be studied was divided into five equal parts so that for each culture studied there was one grown on the basic medium only; another with the same basic medium to which heteroauxin was added; and the other three contained one of the carcinogens at a given level of concentration. The

five differently treated fragments of the same tissue mass constituted a series. By repeated divisions of similar clonal cultures, their number was built up so that there were as many as 20 or more controls and 20 or more cultures each growing on a plant growth substance and on one of the chemical carcinogens.

Transplants were generally made at intervals of five to seven weeks; some few were made after longer periods. The series of cultures was photographed at frequent intervals for purposes of record. The cultures were exposed to subdued light and the temperature ranged from 23° C to 28° C throughout the year.

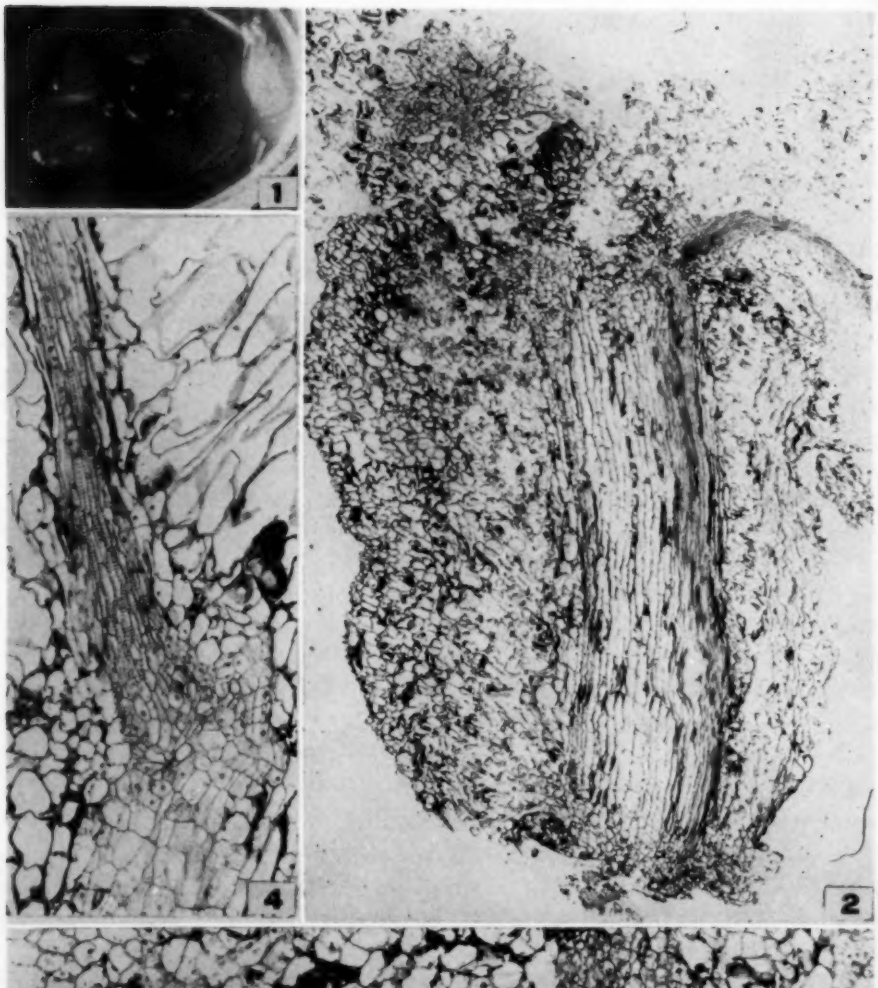
Material was fixed in one of several fixing fluids. Bouin's fixative was used routinely. Flemming's weaker solution and Carnoy's fixative were also used. The tissue was imbedded in paraffin and sections from 5 to 10 μ were cut and stained by Flemming's triple method. Some of these tissues were studied *in toto* by the orcein acetic acid smear technique.

Sunflower Tissue Callus. Sixty internodal segments of seedling stems were started on a basic medium in 125 ml. Erlenmeyer flasks with as many as six segments to the flask. Within a period of a month the tissues were transferred three to four times and the growing fragments had been separated so that each fragment was in 25 ml. of the same nutrient agar in a 125 ml. flask.

Growth of the segments occurred from the cut surface of the tissue and frequently as shown in sections of this material the outer layer of tissue of the inoculum now freed of its epidermis proliferated. The tissue on the cut surface grew out from the cambium region as a jelly-like finely nodular water colored mass. The growth was not uniform for soon minute spherical masses appeared and covered the entire surface of the tissue and finally reached the surface of the agar. Such new growths were separated from the inoculum and the progress of several clones of this type of growth is given to typify the changes in all.

Figure 1 represents an inoculum, 61 with the new growth proceeding from apical surfaces of the cut segments. These were grown on White's basic medium in which ferric citrate was used as the source or iron. The fragments swelled several days after seeding, but no other effect was noted. The figure shows that the new tissue mass had reached the agar, and the black portion is the original inoculum. These cultures were started on Jan. 1, 1947 and on April 7 were transferred to White's basic medium with 0.3 mg. per cent of indole acetic acid.

Section of these primary cultures reveals changes in the exposed cortex (fig. 2). The inner layer of the tissue shows evidence of cell dissociation, while the outer layer has proliferated slightly. The main region of growth occurs in the cambium on both cut surfaces of the segment with the greater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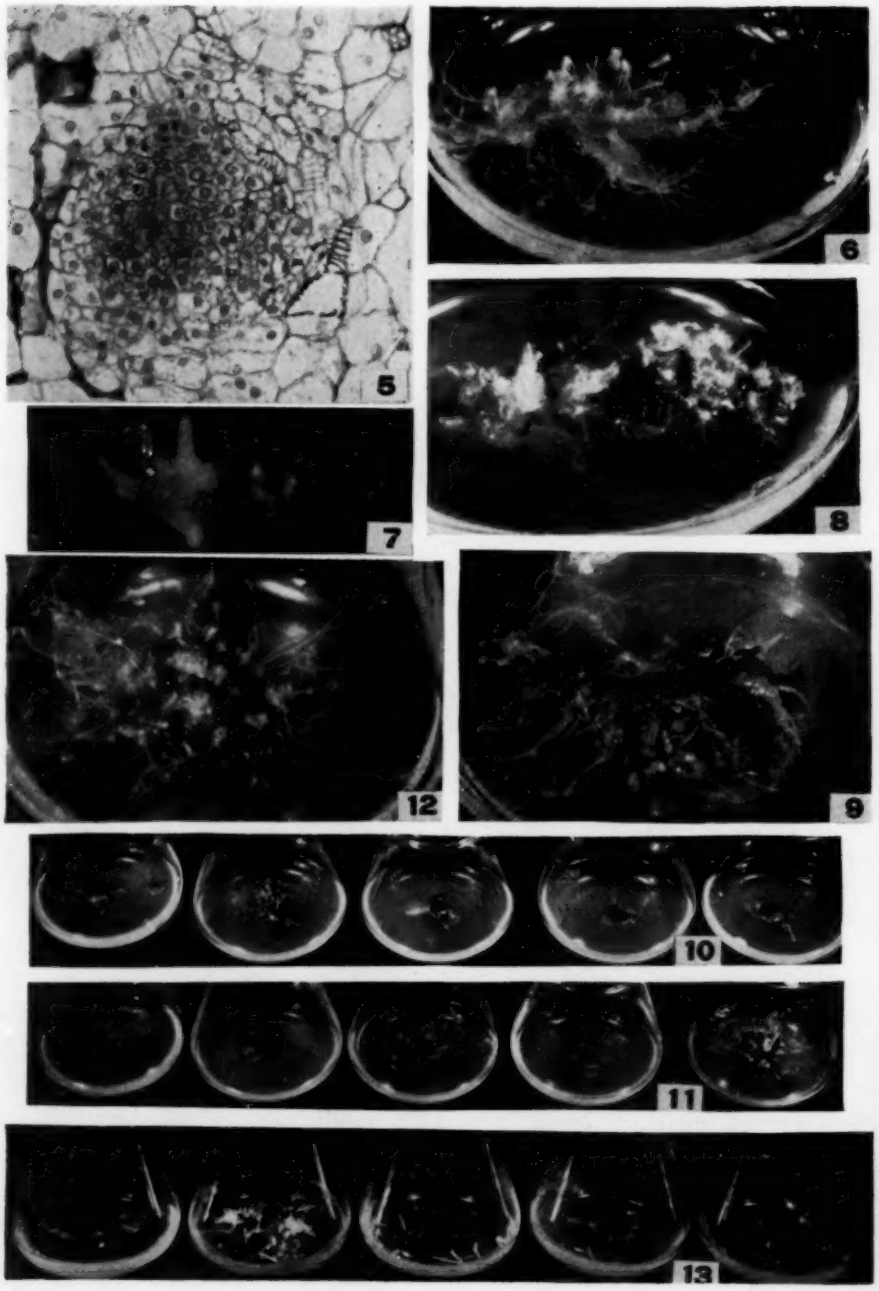
activity at the apical end. The cells in the cambium have given rise to a nodule of tissue consisting of centers of embryonic cells with large nuclei surrounded by cells of variable sizes. The nuclei are small but apparently normal. Lignified cells, small in size, with annular markings, are distributed through the tissue (fig. 3). At the right in the photograph, the cambium has grown out into a strand of fibrovascular elements. This is surrounded by a mass of hypertrophied, elongated cells as shown in figure 4. It was noted that many of the elongated cells had a tendency to collapse. Sections through similarly treated segments (fig. 5) revealed root initials on the inner layers of the cortex arising from a zone of cells along the cambium. In cross sections these root initials appeared normal though division figures were not observed. The surrounding cells seemed disoriented, hypertrophied and several showed spiral lignified markings.

Callus tissues removed from such segments were planted on nutrient agar which consisted of a basic substrate with NAA at 0.1 mg. per cent, or IAA at 0.5 mg. per cent. Clone 10 was started on June 16, 1947 and transferred to Ws with IAA on Oct. 23, 1946 (fig. 6). The new growth developed roots which became progressively covered with a transluscent jelly-like mass. Roots that penetrated the medium branched frequently and behaved normally. Those that emerged from the surface of the explant formed perfect coverings of root-hairs. This is shown in an early stage in clone 7. This culture was planted on June 17, 1946 and photographed one month later (fig. 7). In the carrot no such aerial roots were observed but the fuzzy roots that penetrated the agar were shown to be due to the unusual development of their epidermal cells.

In another tissue mass started approximately the same time, clone 10_4, the culture was carried though six passages. The last one was made on March 3, 1947 and photographed five weeks later, showing the brown explant and the new growth of roots (fig. 8) which developed from it.

A similar clone in series 9, grown on a basic substrate in which 0.1 mg. per cent NAA was incorporated, consisted of a dark brown tissue mass with new growth about the bases of the newly formed roots. These new growths were transluscent and jelly-like in appearance in their early stages. Later, as they aged, they became opaque and brown in color. Frequently entire roots became covered with this new growth and only the terminal portions of some of them showed evidence of root hairs (fig. 9).

FIGS. 1–4. FIG. 1. New growth from segment of sunflower stem seeded 1-10-47, transferred on 4-7-47 to Ws with 0.3 mg percent IAA. Photographed 5-24-47. ×1¼. FIG. 2. Longitudinal section of segment shown in Fig. 1. ×15. FIG. 3. Part of outgrowth from upper left portion of fragment shown in Fig. 1. Note centers of embryonic cells with lignified cells of fibrovascular elements. ×75. FIG. 4. Part of Fig. 1, the upper right showing development of a strand of tissue with fibrovascular elements. Note the hypertrophied cells which arise from the cortical portion of the strand. ×75.



FIGS. 5–13. FIG. 5. Part of segment of sunflower stem showing section of root initial. × 190. FIG. 6. Clone 10 grown on IAA from 10-23-46 to 12-6-46. The explant developed

The Effect of the Carcinogens. These and similar clones were divided and seeded on a basic medium Ws, Wt, or Wsf in which the carcinogens were incorporated.

Culture 7_6 was grown on basic medium Wt. It was divided on May 5, 1947 to establish a series of clones. Figure 10 shows such a series photographed on July 2, 1947. All the flasks contained a basic medium. The first flask served as control and contained Wt only. The second contained Wt plus IAA 0.5 mg. per cent and each of the following three had, in order mentioned, Wt plus D 0.07 mg. per cent; Wt plus B 0.12 mg. per cent and Wt plus M 0.12 mg. per cent. The normal culture and those growing on the three carcinogens grew slowly but each formed a small number of roots. The growth was dark brown in color and the tissue mass assumed an opaque jelly-like consistency. A number of aerial roots appeared with a coating of root hairs. The methylcholanthrene culture had long thick brown colored roots. The indole acetic acid culture grew best. It was characterized by numerous aerial fuzzy roots.

The growth appeared to be a function of the indole acetic acid. Growth of the carcinogen treated cultures was not better than the control. These observations were made on a number of cultures of different clones under the same conditions. However, when culture 7_62, grown on Ws medium with indole acetic acid, was divided and the subcultures were seeded on the same basic medium with the concentration of the carcinogens unchanged, the growth in the D and M cultures was more than thrice the size of those of the control and the Ws plus IAA as shown in figure 11. The control produced a small opaque tissue mass with several roots unaffected by its previous growth on IAA. The second culture on IAA produced fibrous roots with several aerial ones. Only the culture on B showed a lag in growth of the tissue mass. Its fibrous roots were few but long. The D and M cultures

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roots which became covered progressively by a jelly-like tissue. Aerial roots have a fuzzy covering of root hairs. $\times \frac{3}{4}$. FIG. 7. Clone 7, early stage in the growth of explant, roots covered by long hairs. $\times \frac{1}{4}$. FIG. 8. Clone 4 after the sixth passage, started 6-17-46 on Ws with NAA 0.5 mg percent. Last subculture made on Wt with IAA 0.5 mg percent on 3-3-47, photographed 4-11-47. $\times 1\frac{1}{4}$. FIG. 9. Culture 9_1 grown on Ws with 0.1 mg percent NAA. Last passage was made 5-1-47, photographed 7-2-47. The tissue is the black portion from which thick isolated masses of new growth have arisen about the roots. $\times 1\frac{1}{4}$. FIG. 10. Culture 7_6 grown on Wt medium divided to form five subcultures; from left to right, Wt; Wt plus IAA 0.5 mg percent; Wt plus D 0.07 mg percent; Wt plus B 0.12 mg percent; Wt plus M 0.12 mg percent. $\times \frac{3}{4}$. FIG. 11. Culture 7_62 on Ws with IAA divided to form five subcultures; left to right, Ws; Ws IAA 0.5 mg percent; Ws with carcinogens D, B, M, as used in cultures shown in Fig. 10. Note growth on D and M treated cultures. $\times \frac{3}{4}$. FIG. 12. Culture M shown in Fig. 11. Note the aerial roots and the branching fibrous roots in the substrate. $\times 1\frac{1}{3}$. FIG. 13. Culture series 221 grown on Wsf medium. The first and second cultures were grown on Wsf and Wsf IAA respectively for the last five passages. The next three cultures were derived from an IAA culture and are shown after growth from 9-28-48 to 11-15-48 on Wsf plus D; Wsf plus B and Wsf plus M at concentrations of 5 mg percent each. $\times 1\frac{1}{3}$.

seemed to show a stimulative effect of these chemicals. The transplants were made so that the agar adhering to the roots was carefully removed and very little if any of the original agar was transferred with the division of the tissue. This would indicate that the tissue acquired some growth stimulus from the IAA and this was enhanced by the D and M in the concentrations used. The culture on B reacted poorly to this carcinogen. Figure 12 shows a view of the culture grown on M. Note the aerial surface roots and the branching roots that penetrated the agar.

Culture 221 was started on April 19, 1946. This was transferred and subcultured at intervals of 5 to 8 weeks. The control culture prior to Sept. 28, 1948 had been on a basic medium for 4 passages and the IAA treated culture was on this medium for 4 previous passages. These two cultures were divided into 4 equal parts and transplanted. Only one of the fragments grown on the basic medium was transplanted to Wsf medium. The four fragments grown on IAA were set out on Wsf plus IAA 0.5 mg. per cent; Wsf plus D 5 mg. per cent; Wsf plus B 5 mg. per cent; and Wsf plus M 5 mg. per cent.

On November 15, 1948 these cultures were photographed and are shown in figure 13. The control shows a blackened tissue mass with few roots. All three carcinogen treated cultures had new growth of gelatinous material which was most marked in the WsfM culture. The terminal portions of the roots that emerged above the agar as its edges were covered with white root hairs. The IAA treated culture was heavily covered with roots and white root hairs.

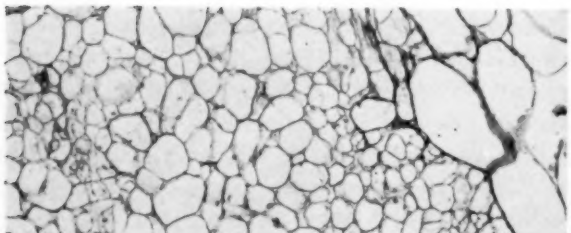
It appears that the repeated doses of IAA enable the culture to put out more roots than those treated with the carcinogens, even though the concentration of the chemical carcinogens was increased manifold. The sunflower tissue does not habituate itself to IAA as suggested by Gautheret (1945) for carrot root tissue. The carrot tissue fails to respond to repeated stimulations of this chemical at low concentration. The IAA used in these studies invariably called for a reaction from the sunflower tissue mass to root formation with the accumulation of a jelly-like mass of tissue about the bases of the roots.

The Cytology of the Sunflower Callus. Microscopical studies of these sunflower callus tissues grown on basic medium show the mass to be made up of parenchymatous cells. Large cells occupy the periphery of the growth common to the carrot tissue mass. These cells also have a sparse cytoplasm which occupies a narrow margin about the cell wall, and a few small nuclei poorly differentiated may to be seen. The interior of the tissue mass is made up of cells of variable size. The smaller cells contain a centrally placed nucleus in a fine granular lacework of cytoplasm. No lignified cells with markings were noted in the tissue. Figure 14 shows a section of such a tissue mass and was made from clone 7_6, 17 weeks after the culture was started.

Microscopical sections of treated cultures showed root elements with dissociation of the epidermal and cortical cells. The IAA treated cultures studied showed uniformly branched roots with definitely organized bodies which took their origin from the cells near the elongated cells that formed the conducting system. Figure 15 is a section of a sunflower tissue mass with 5 to 6 organized tissue masses. The whole is surrounded by loose cells, many of which are collapsed. In a view under high magnification (fig. 16) a rudimentary conducting system is seen with four globular masses of tissue arising along the elongated cells, which appear to be made of conducting elements although no marked tracheids or vessels *per se* are to be seen. The globular masses are composed of small cells with faintly staining nuclei. The central part of the mass is composed of definitely oriented cells at the base or point of attachment to the root. The whole seems to be enveloped in a layer of tissue four to five cells in depth. Here there are no evidences of crown gall-like tissue, such as is commonly seen in the carrot tissue after treatment with the chemical carcinogens. These appear to be root initials which have been altered by the treatment. These structures have been observed in sections of a number of cultures studied.

The tissue subjected to the chemical carcinogens was studied microscopically. In these cultures the tissue masses as indicated in the gross photographs were associated with abundance of roots. Sections invariably showed cell dissociation with hypertrophy of the cortical and meristem cells to form elongated club shaped structures. Figure 17 shows a section of a part of a culture grown on methylcholanthrene for more than five weeks. The conducting system in this branched root appears normal. The major part of the tissue about the central cylinder is hypertrophied. The cells in some parts are loose or may form simple chains. A part of this tissue under higher magnification is shown in figure 18. The fibrovascular elements appear normal but the immediately surrounding generative tissue shows active division with differentiation of lignified marked cells. The cortical cells that have elongated appear empty except for fine strands of cytoplasm along the cell wall.

Beside the differentiation of roots from this tissue, no other organs have appeared although the tissues were subjected to the same treatment given carrot and tobacco tissues. The evidence is rather clear that the chemical agents enhance the existing potentialities of the tissue to differentiate. Apparently lacking in this property the carcinogens have been without value on sunflower cultures in bringing out stem and leaf development. The aberrant cellular phenomena observed in the carrot giving it the appearance of crown gall tissue after growth with carcinogens or the heteroauxin has not been observed in this tissue. These sunflower tissue cultures have been under investigation for the past three years and further study is in progress.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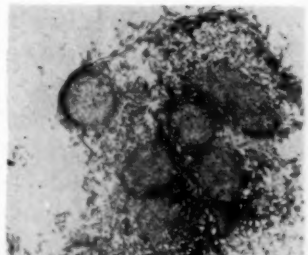
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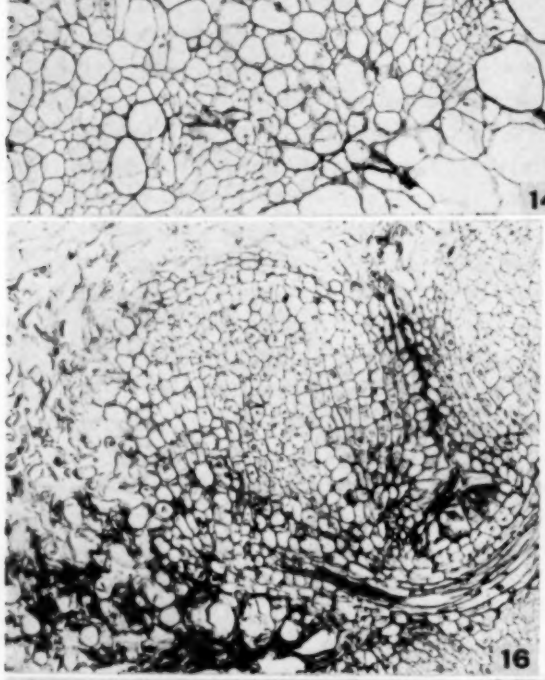
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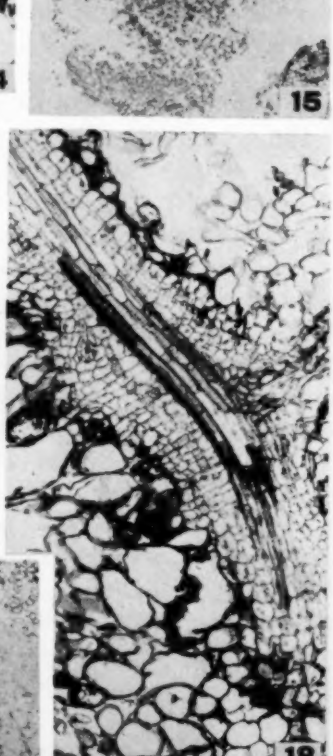
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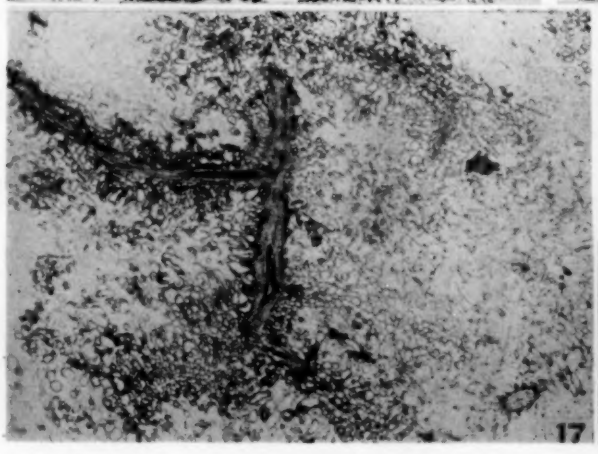
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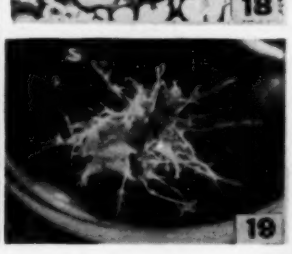
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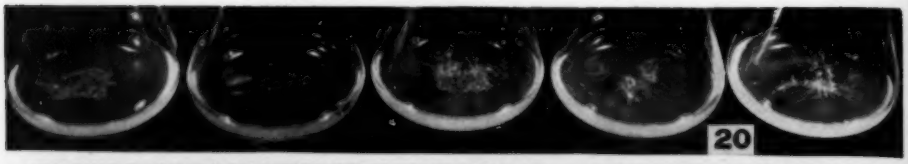
The Tobacco Segment and Callus. The *in vitro* culture of five species of tobacco was studied. The growth and development of these tissues was variable, for some formed true tissue cultures, like *N. Langsdorffii* and *N. affinis*, and produced from the tissue mass and roots, shoots and leaves, complete plants, while another species, *N. tabacum*, produced small callus from the seeded segments and before this had developed sufficiently, leaf buds and roots appeared from the meristem and finally complete plants were formed. These plants were separable from the segment and grew independently on nutritive agar medium. Plantlets also developed from the exposed surface of the segments of *N. Langsdorffii* long after a tissue mass had formed. The other two species, *N. glauca* and *N. glutinosa*, produced tissue masses of slow growing capacity. Their segments failed to produce buds as occurred in the other tobaccos. The calluses produced by segments of these tobaccos are in culture and some detail of their growth is reported.

N. Langsdorffii. Cultures of *N. Langsdorffii* were started in the latter part of 1946. Callus growth was obtained from the soft apical portion of the stem used before flowering had occurred. These shoots were removed from plants grown in the garden; the outer epidermis was removed and 4 segments were seeded in each of eight 125 ml. flasks on five different media: Ws; Wt; Wt with iron citrate, Wt IAA 0.5 mg. per cent and Ws IAA 0.5 mg. per cent. Initial growths were obtained on the Wt medium with IAA. Of 32 inocula 12 succeeded in growing satisfactorily 44 days after planting. Of this number 4 were selected because of their greater activity and by April 10, 1947 (72 days later) the inocula were separated. The other cultures were discarded, for lack of growth. It seemed that the additional IAA was needed for continued growth of the callus. Some segments produced roots but none produced leaf buds.

On June 5, 1947 the calluses of the cultures grown on Wt plus IAA were extensive and had covered the original inoculum completely. This new growth was translucent and covered with many white aerial roots with root hairs. This view of the tobacco callus presented many similarities with that of the sunflower outgrowth though the tawny color of the former was quite different from the dark brown color of the latter. The callus tissue was separated from the stem segments; they were divided into five equal parts and seeded on Ws as the basic medium; IAA 0.5 mg. per cent was added to the second of each

FIGS. 14–19. FIG. 14. Section of clone 7_6, consisting of parenchymatous cells, 17 weeks after growth was started. ×75. FIG. 15. Part of clone 7_2 grown on Wt with 0.5 mg percent IAA. Last transfer 4-28-47; fixed 7-23-47. ×15. FIG. 16. Portion of Fig. 15 showing an aberrant tissue mass. ×75. FIG. 17. Section of clone 7_4 grown on Wt with M. Last transfer 5-5-47, fixed 7-23-47. ×15. FIG. 18. Part of Fig. 17. ×75. FIG. 19. Subculture from a stem segment of *N. Langsdorffii* 6 months after planting on IAA through five transplants. Growing on Ws with NAA 0.01 mg percent. ×¾.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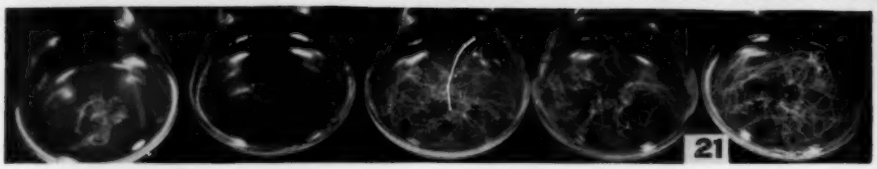
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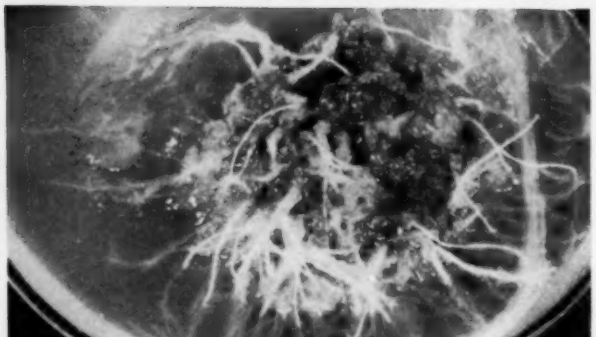
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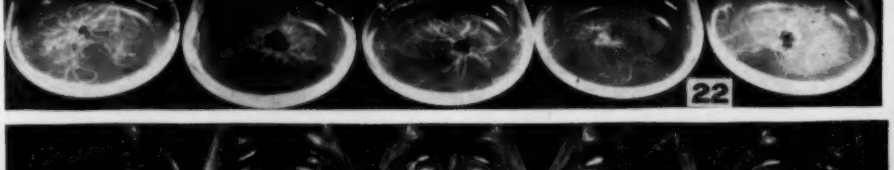
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of a series of cultures and D,B, and M at the level of 0.1 mg. per cent was added to the remaining three cultures in each group.

Other tissue masses were treated similarly with the difference that the carcinogens varied in concentration level up to and including 5 mg. per cent. Subcultures were made from those grown on the basic medium as well as from those grown on the carcinogens so that possible residual effects on growth could be detected. As many as 200 cultures of the tissue were studied with the IAA, the carconogens and controls. In the concentration of the carcinogens used, no toxic effect was noted. Root growth seemed to be increased on the carcinogens D and M following growth on medium with IAA. Differentiation of complete plantlets occurred on media with the carcinogen D as on the Ws or Wt basic media.

Here it will suffice to present the reactions of a selected group of these cultures. In figure 19 a culture of *N. Langsdorffii* started January 18, 1947 is shown on Ws medium with NAA at a concentration of 0.01 mg. per cent. The jelly-like growths, not unlike those seen in sunflower cultures, take the form of papillae which terminate in short roots. Similar tissue masses have been produced by planting fibrous roots on the medium with heteroauxin. The culture shown in figure 19 was divided and seeded on Ws: Ws IAA 0.5 mg. per cent; and Ws medium with D,B,M, each at a level of 0.1 mg. per cent.

The culture with the basic medium and the culture with the heteroauxin showed comparatively little growth after 43 days. The cultures bearing the carcinogens showed growth of tissue mass with prolific root growth. This culture was not transplanted, but its subsequent development was followed (fig. 20). It appears that the control and the IAA culture failed to grow, but the carcinogen treated cultures nevertheless indicated continued root growth as shown in figure 21 photographed 41 days later. The best growth response is on the medium with D, then that on the medium with M and finally the growth on B. The possibility that these reactions may be due to a carry-over of the IAA is invalid; IAA appears unstable and the differences in reactions of the tissue on the carcinogens are evident. The continuous

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FIGS 20–26. FIG. 20. Series of cultures of *N. Langsdorffii*, left to right, grown on Ws; Ws plus IAA 0.5 mg percent; Ws plus D, Ws plus B, Ws plus M, each at 0.1 mg percent for 43 days. $\times \frac{3}{8}$. FIG. 21. The same cultures 41 days later. $\times \frac{3}{8}$. FIG. 22. Series of cultures of *N. Langsdorffii* started 1-18-47, last division made 6-18-47, grown on (left to right) Ws; Ws IAA 0.5 mg percent, the carcinogens D, B, M, in one of each at 0.3 mg percent, photographed 8-28-47. $\times \frac{3}{8}$. FIG. 23. The same cultures shown in Fig. 22, photographed 10-3-47. Differentiation of planlet from periphery of tissue mass on culture with D. $\times \frac{3}{8}$. FIG. 24. Plantlet separated and grown independantly on nutrient agar. 11-15-47. $\times \frac{3}{8}$. FIG. 25. Tissue derived from segment of a stem of *N. affinis* started 8-24-47, photographed 12-22-47. $\times 1\frac{1}{4}$. FIG. 26. Another culture of the same grown on Wt IAA 0.5 mg percent. Last transfer 4-30-48, photographed 7-9-48. Note opaque tissue mass with elongated papillae with long white branching roots. $\times 1\frac{1}{4}$.

and successful growth of these cultures for 84 days on the same substrate indicates that cultures under the prevailing conditions in this laboratory do well for at least 8 to 9 weeks.

Another clone of *N. Langsdorffii* callus started June 18, 1947 was subcultured and grown on a Ws substrate in which the carcinogens had been increased to 0.3 mg. per cent. A photograph of this series was made on August 28, 1948 (fig. 22). The growth of the tissue masses in these cultures was approximately equal although the root growths in the third flask with D and in the fifth flask with M are more extensive. These cultures were likewise permitted to grow undisturbed, and photographed again on Oct. 3, 1947. Figure 23 shows several points of interest. The control has not changed, but the IAA culture has increased its tissue mass and many more short roots have appeared. The B and M cultures have increased slightly in tissue mass and in length and number of their roots. The D culture third from left developed a plantlet from the periphery of the tissue mass. This structure consisted of pale green shoot with spirally arranged leaves on it. Though not fully developed, the leaves bore close resemblance to the leaves of this species of tobacco. This differentiation of a plantlet from the tissue mass or roots which it formed occurred nine months after the culture was started and during which time it went through 4 passages. It is not assumed that the carcinogens induced this growth but it is obvious that the carcinogen D did not interfer with its development and it may possibly have enhanced it. In a study now in progress fibrous roots of *N. affinis* have developed tissue masses similar to the one shown in figure 19 and after several months of growth have developed typical shoots. The cultures of callus tissue of *N. Langsdorffii* that produced fully developed plantlets, were not as numerous as those of the carrot. Subdivision of this culture did not increase the number of plantlets materially. The plantlets were isolated (fig. 24) and grown on a nutrient agar.

Some segments of stems of *N. Langsdorffii* grown on basic Wsf medium showed very little proliferation from their cut apical surfaces, but leaf buds from the periphery of the surface were formed within a month. Although these plantlets developed roots they seemed to depend on the contents of the segments for they failed to grow. This type of development is most common on *N. tabacum* segments as indicated below.

Sections of inocula seeded on medium with IAA were studied for the seat of the morphological change and subsequent growth that occurred. A longitudinal median section through a segment of the stem showed that growth takes place over the apical end of the segment, near the region of the meristem and became confluent with cortical tissue proliferation, along its vertical wall. At the outer cambium the cells were small, active, and several organ initials, still submerged, developed in the new loose parenchymatous

tissue. The upper surface growth was restricted to small areas forming a crown of tissue comprised of active small cells, as observed by Gautheret (1945) in the segments of a number of fleshy roots.

A more detailed study of these organ initials revealed serially arranged cells making a uniform layer about the new growths. In this layer lignified cells with reticulate markings are found yet most of the cells are large with well differentiated nuclei. Chloroplasts appear in some of them. Along the outer wall of this surrounding tissue the cells become more irregular while in the interior the cells are loose and hypertrophied. The many organ-initials were cut at different levels and clearly show cells embryonic in character. They are small with comparatively large well-differentiated nuclei.

Sections of tissue masses which were tested with the carcinogens represent partially organized structures with loose tissue and were suggestive of the figures noted in the sunflower callus. The loose, collapsed and hypertrophied cells were not as common as they were in the sunflower.

N. affinis. Segments of young succulent stems of this tobacco were prepared on August 24, 1947 in a manner already described for *N. Langsdorffii* and were set on basic medium Wt. Callus growths were procured only from the segments on the latter medium and figure 25 represents one of the successful growths obtained four months after seeding. During this period the inoculum was transferred to fresh medium three times. The inoculum shown in this figure is completely overgrown by callus tissue and may be recognized in the center as the darker portion of the growth. The centers of proliferation are numerous and have given the tissue mass an irregular outline. Few papillae appeared in this tissue such as were seen in the *N. Langsdorffii* growths. The consistency of the tissue mass appeared to be the same in both and difficulty was experienced in separating them on inspection. Roots appeared from the upper surface in some of the cultures of *N. affinis* and their terminal portions were covered by long root-hairs.

These new portions of the callus growth were separated from the original segments and the parts were planted on Wsf or Wsf with IAA on Dec. 23, 1947. The tissue that was transferred to the medium without the IAA grew as actively as the others, although precautions were taken to remove all traces of IAA agar in the transfer of the tissue. The growths were rapid and on Feb. 3, 1948 the cultures were transferred again. Little change occurred in the nature of the growths, on Mar. 17, 1948, yet some showed a small number of roots not unlike the mother culture. This absence of roots may indicate an adaption to the influence of IAA; the concentration was maintained at 0.5 mg. per cent. Of those cultures with roots, '4_1a' was transferred to Wt IAA on Mar. 17, 1948 and on April 30, 1948. Figure 26 represents a culture from the April transfer on July 9, 1948. The tissue mass was covered in part

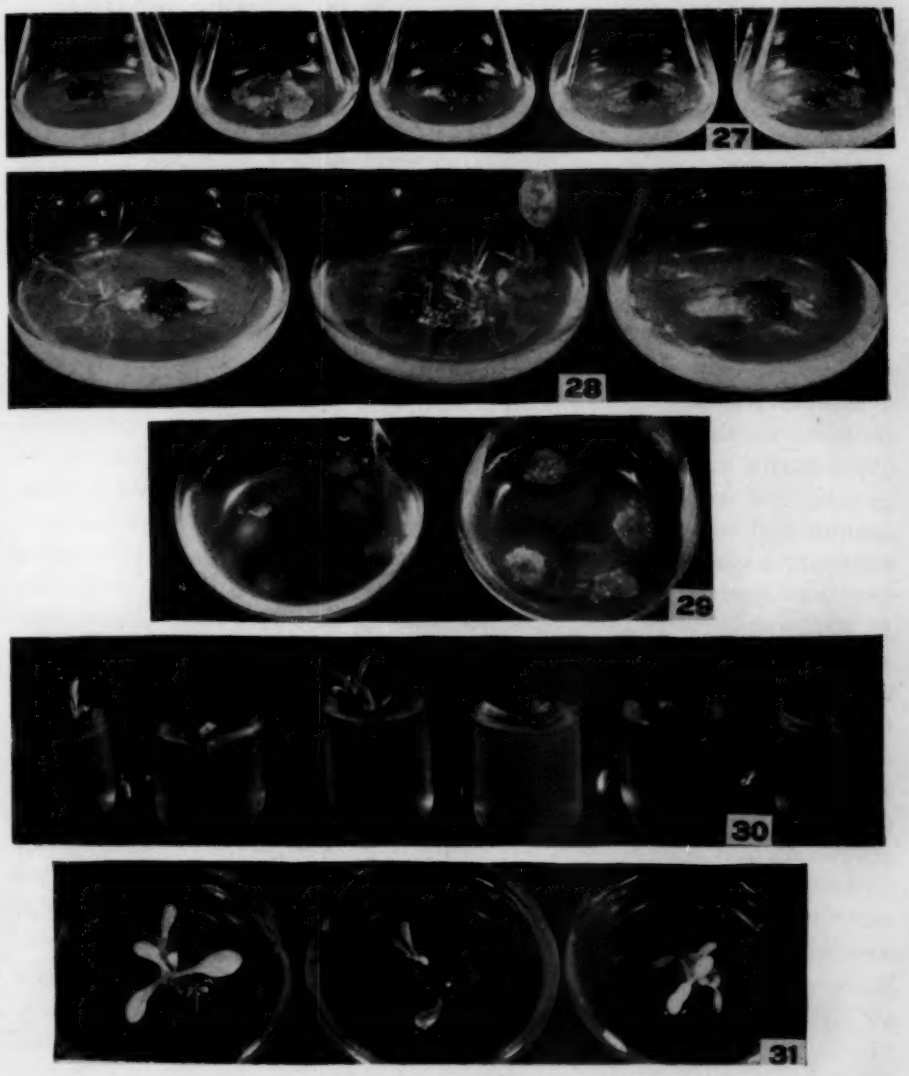
by an extensive growth of roots from its upper surface. The tissue mass was nodular, opaque, and the surface papilae from which the roots arose were elongated.

Selected clones of these cultures were subdivided and set out in a series of cultures which consisted of the basic medium with IAA; D; B; and M. While these studies are still in progress it seems of interest to present the reactions observed in some of these cultures at this time. Figure 27 shows series '4_1c' in which the growth is preponderantly heavy in the second culture (Wt IAA). The carcinogen treated cultures at the concentration of 5 mg. per cent and the control were viable. No gross macroscopical changes occurred although the rate of growth was not unlike that of the control. No differentiation occurred and no roots were formed in these subcultures.

Of the root forming cultures, the series 4_1b is shown in part in figure 28. The IAA and the B cultures were eliminated and the control Wsf, Wsf plus D and M 5 mg. per cent are shown. In the control medium and in the D culture fully differentiated plantlets developed. In the D culture the origin of the plantlets is not clear but seems to have arisen from the tissue mass. In the control the stem with undeveloped leaves take their origin from a bud on the root. It has been pointed out above that IAA at the concentration used seems to act as a precursor to cauline and foliar differentiation. Growth of the tobacco and carrot tissues is made possible by the heteroauxin and the physiological and morphological bases for complete differentiation seem to take place during the growth of the tissue on the heteroauxin medium. The removal of the heteroauxin permits growth and differentiation to ensue, yet continued growth of a carrot culture on IAA requires several passages on the basic medium before differentiation is resumed. In large cultures of carrot tissue when growth appears above the substrate, complete differentiation may occur even though heteroauxin was included in the medium. The concentration of indole acetic acid has been studied by Gautheret (1945) and the various concentrations from 10^{-4} to 10^{-11} show overlapping reactions in the cultures. The concentration (5×10^{-6}) used principally in these studies suggests the possibility of its involvement in the process of differentiation. The present study and one in progress now indicate that in *N. affinis* the new shoots may arise in some instances from the preformed roots induced by the IAA. The dibenzanthracene seems to have an enhancing effect upon the growth and differentiation of the tissue.

N. tabacum. Segments of stems of these plants were prepared by washing the stems in water and rinsing them in 70 per cent alcohol before removing the outer epidermis. The axillary stems of *N. tabacum* var. *burley* were used when the plant had attained the height of three to four feet. This tissue was soft and well adapted to this use. Small segments and quadrants of large

segments were planted on Wt medium. The apical portions of stem *N. glauca* and *N. glutinosa* were started in the same manner.



FIGS. 27–31. FIG. 27. Series of cultures grown on Wt, Wt IAA, Wt D, Wt B, and Wt M, the carcinogens at 5 mg percent. Note growth on second culture with IAA. × ⅔. FIG. 28. A part of a series of *N. affinis* cultures, first control on Wsf medium, second on Wsf plus D and third on Wsf plus M. Early differentiation of plantlets on Wsf and Wsf D. × ⅔ FIG. 29. Segments of *N. tabacum* grown on Wt with IAA, started 8-8-47 and photographed 8-28-47. × ½. FIG. 30. Segments of stems of *N. tabacum* grown on basic medim 20 days after seeding. × ⅔. FIG. 31. Segments with plantlet development, no roots are present. × ½.

Cultures of *N. glauca* and *N. glutinosa* presented no new phase other than that observed in *N. affinis* or *N. Langsdorffii*, yet no segment developed leaf buds or shoots. The tissue masses appeared on the apical cut surfaces of the segments and have been growing slowly since Aug. 1947 when they were started. Though incomplete, the data furnish a sharp contrast with the other species of tobacco studied and are worth noting at this time.

Segments of *N. tabacum* presented responses to cultivation that were different and of interest. Whole segments, are shown in figure 29, started on Wt medium in which IAA was included. The first reaction consisted of proliferations along the periphery of the cut surface and after three weeks the entire upper surface was covered by callus which consisted of minute watery globular bodies. The growths were not uniformly developed in all segments. The segments seeded on the Wt medium that was free of IAA responded differently. Here the active segments became covered with what appeared to be a white tomentum which grew for a short time only. The intensity of the reaction varied, for some segments became completely covered with this white felt-like structure, while others showed little or no growth. The actively growing segments were transferred to Wt or Wsf medium and bud proliferation ensued. Figure 30 shows a group of selected segments in test tubes grown on Wt medium 9 weeks (Oct. 11, 1947) after they were first seeded. The growth of the new shoots was rapid and on Nov. 15, 1947 well developed shoots had formed (fig. 31). Some of the leaves were perfectly green while others were entirely white. In still a third group of these shoots, only one or two leaves were white or partially green. It is of interest to note that the stems and their leaves formed on the margin of the cut surface of the segments and on their walls. While no roots were formed at first from the segments or developing buds, they appeared from the lower portion of the stems of these new plants after the leaves were fairly well grown. At that time some of the plantlets were separated from the stem segments and transferred to test tubes where they continued to grow for many months when they were preserved. The observation on the development of plantlets from internodal segments of the tobacco is in accord with Skoog and Tsui (1948), but a large number of segments developed plants on basic Wt or Wsf without the addition of chemicals these authors used. The segments grown on the basic media gave no evidence of growth. The surface tomentum became dingy in color but formed no true callus. These tissues were transferred several times to fresh substrate but failed to grow and were later discarded.

The tissues started on media with IAA produced a tissue mass on the apical surface of the segments. It morphological characteristics were not unlike those of the other species of tobacco mentioned above, but without

roots. The callus darkened with the succeeding passages and showed little activity. At present this tissue has not been subjected to carcinogens.

The significance of the bud development of *N. tabacum* segments grown on a substrate without the addition of IAA to the medium, indicates some function of the IAA. In this type of tissue culture it suggest that the heteroauxin inhibits cauline and foliar development (Skoog & Cheng Tsui 1948).

SUMMARY AND CONCLUSIONS

Normal stem segments of the seedling sunflower, when grown on White's basic medium, produce a translucent water colored callus. This growth encircles the cambium zone and finally covers the segment and extends to the surface of the medium. Secondary root initials are produced from the inoculum.

Segments grown on the basic media which include indole acetic acid (IAA) at a concentration of 0.5 mg. per cent, produced roots which became covered with a down attributable to epidermal proliferation like root-hairs. The roots which grew through the substrate became covered by a translucent mass which tended to mat formation.

Fragments of the sunflower tissue mass were exposed to various concentrations of the carcinogens 1,2,5,6-dibenzanthracene (D); 3,4-benzpyrene (B); and 20-methylcholanthrene (M) in slow gradients from 0.1 mg. per cent to 5.0 mg. per cent. No reaction that could be construed as tumor or malignant growth appeared. The carcinogens enhanced the growth of the roots and sustained the growth of the tissue mass.

The histological studies of these treated tissues revealed no atypical cells such as appear in the carrot cultures under similar conditions.

Segments of normal shoots of *N. Langsdorffii*, *N. affinis* and the axillary branches *N. tabacum*, *N. glutinosa* and *N. glauca* were cultivated on basic media.

On media with IAA callus formation occurs from the inoculum which forms roots early and behaves like the sunflower cultures.

Fragments of these outgrowths were systematically divided and placed on medium like that used for carrot and sunflower tissue masses.

The carcinogens produced no toxic effects even at the highest concentrations used. Growth of the roots was accelerated but the tissue masses increased only slightly in size. The mat formation of the roots gave the impression of increased tissue mass.

Culture of the tissue mass of *N. Langsdorffii* and *N. affinis* produced complete plantlets. These arose on the basis of the tissue mass and from roots that developed from the tissue mass. These differentiations occurred in cultures on media which contained a carcinogen.

This growth was not directly attributable to the carcinogen, but the evi-

dence is clear that these chemicals did not interfere with the tendency to bud development.

Segments of *N. tabacum* grown on basic medium behave differently from those placed on a similar medium with IAA. Buds are developed in the former group after a white tomentum begins to cover the apical surface of the segment. These buds develop into shoots with leaves and subsequently develop roots.

The effects of the carcinogens on this species of tobacco together with *N. glutinosa* and *N. glauca* are still in process of investigation.

Plant tissues subjected to extremely high concentrations of the chemical carcinogens as compared to lower plant and animal forms or specialized cells, such as the fibroblasts of the mammal and bird, show increased growth reaction in tissue mass and roots with frequent occurrence of complete differentiation.

Malignant tissue masses judged on the basis of excessive growth with the concommitant increase in volume and weight, are not induced in these plants by the carcinogens.

The studies of Gautheret and Nobécourt and their associates indicate the importance of indole acetic acid to the growth *in vitro* of normal plant tissues. In the present studies the level of concentration of this growth substance (0.5 mg. per cent) seems to induce morphological changes that ultimately lead to bud formation. That buds fail to develop in its presence seems evident from the work of Skoog (1944) on tobacco hybrid overgrowths, the callus on normal segments of the common tobacco (1948) and on the tissues reported here.

The tendency of the overgrowth of the hybrid tobacco is to form leafy structures *in situ*. The common tobacco shows a tendency to leafy crown gall development when inoculated with *P. tumefaciens* (Levine 1923). Normal stem segments of the tobacco grown *in vitro* show the same tendency to produce leafy shoots. Only a small number of carrot root segments now in culture produced shoots one year after seeding and after six transfers to basic media.

The cultures of carrot tap root callus grown on basic media failed to produce plantlets, but after what appeared to be a conditioning process induced by heteroauxin fully developed plantlets appeared following a transfer to a basic medium. It seems as though the heteroauxin (IAA) delays bud development because it interferes with some substance necessary to the process. This substance appears to be abundant in the tobacco segments but lacking, or in too low a concentration, in the carrot tissue to effect bud development. The IAA initiates morphological changes in the carrot which in turn induce the necessary bud differentiation substances to develop. Prolonged treatment with IAA at a given concentration effects the

morphological changes but impairs the development of the necessary bud development factors. The time element appears to have some bearing on these processes. These phases of growth and differentiation of tissue culture material are in progress.

Thanks are due Dr. E. J. Baumann, chemist under whose direction the media used in these studies were prepared.

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BULLETIN OF THE TORREY BOTANICAL CLUB
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FOUR NEW AMERICAN UMBELLIFERAE

MILDRED E. MATHIAS AND LINCOLN CONSTANCE

Of the many interesting specimens of *Umbelliferae* which have been sent to us in recent years, several seem to be worthy of description. Although we have papers in preparation concerning representatives of the family in both North and South America, none of these relates directly to the novelties to be proposed here.

We are indebted to Dr. Rimo Bacigalupi and the late Mr. Charles A. Weatherby for very substantial assistance with the Latin diagnoses.

Ammoselinum Rosengurttii Math. & Const., sp. nov. (fig. 1.) Herba scabra supra basim ramosa 1.5–3 dm. alta; folia ovata ternata pinnatisecta, 2.5 cm. longa, 1.5–3 cm. lata, segmentis ultimis lineari-oblongis linearibusve obtuse mucronulatis 1–10 mm. longis, 0.5–1 mm. latis; petioli 2–5 mm. lati, basi tantum anguste vaginantes; pedunculi 1–4 vel umbellae interdum sessiles; involucrum nullum; involucelli bracteolae lineares 2–7 mm. longi; radii 2–4, inaequales, 2–20 mm. longi; pedicelli 1–4, inaequales, 10 mm. longi vel obsoleti; carpophorum bipartitum; fructus ovoideus vel ovalis, 3–4 mm. longus, 2.5–3 mm. latus, costis dorsalibus acutis scabris, lateralibus suberoso-crassis supra commissuram incurvatis; vittae parvae in valleculis plerumque 3, in commissuris 2; semina facie valde concava.

Branching above the base, 1.5–3 dm. high, scabrous throughout; leaves ovate, 2–5 cm. long, 1.5–3 cm. broad, ternate-pinnately dissected, the ultimate divisions linear-oblong or linear, obtuse, mucronulate, 1–10 mm. long, 0.5–1 mm. broad; petioles 2–5 mm. long, sheathing only at the base, narrowly scarious-margined; peduncles terminal and opposite the leaves, 1–4 cm. long, or some umbels sessile; involucre wanting; involucel of 2–7 linear bractlets 2–7 mm. long, about equaling the pedicels; rays 2–4, unequal, 2–20 mm. long; pedicels 1–4, unequal, 10 mm. long to obsolete; carpophore parted to the base; fruit ovoid to oval, 3–4 mm. long, 2.5–3 mm. broad, the dorsal ribs acute, scabrous (callous-toothed), the lateral with corky appendages incurving over the commissure; oil tubes small, usually 3 in the intervals, 2 on the commissure; seed face markedly concave.

TYPE: URUGUAY. FLORIDA: Pratense, Estancia Rincón de Santa Elena, Picada Castro, Arroyo Mansavillagra, 8 November 1946, *Rosengurtt & Gallinal 5753* (UC No. 753,469; isotype, LA).

Specimens examined: URUGUAY. ARTEGAS: Cuareim, 26 October 1902, *M. B. Berro 2973* (UC). CERRO LARGO: Laderas pratenses, parcela 12, Estancia Palleros, Río Negro, 12 December 1937, *Gallinal, Aragone, Bergalli, Campal & Rosengurtt 1895* (GH). FLORIDA: Laderas pratenses, Zyitria parcela, Estancia Santa Clara, Timote, December 1938, *Gallinal, Aragone, Bergalli, Campal & Rosengurtt 3608* (GH); Laderas pratenses, parcela centro, Rincón, Timote, December 1938, *Gallinal, Aragone, Bergalli, Campal & Rosengurtt 3899* (GH); Pratense, Estancia Rincón de Santa Elena, Picada Castro, Arroyo Mansavillagra, 8 November 1946, *Rosengurtt & Gallinal 5753* (UC: TYPE; LA). PAYSANDÚ: Agronomía, pratense, 6 November 1937, *B. Rosengurtt B 2191* (UC). RÍO NEGRO: Estancia de Goenaga, Rincón de las Gallinas, Arroyo de los Patos, Orillas del Río Uru-

guay, 22–23 October 1942, *B. Rosengurtt B 4112* (UC). SALTO: Pratense, Escuela de Agronomía, San Antonio, *B. Rosengurtt B 4886* (UC). SORIANO: Pratense, Mercedes, 24 November 1936, *Gallinal & Rosengurtt 5980* (UC); Pratense, Santa Elena, Juan Jackson, 24 November 1940, *Gallinal, Aragone, Bergalli, Campal & Rosengurtt PE-4520* (UC).

This remarkable Uruguayan species of a genus previously known only from North America, where it is represented by three species in the southwestern United States and adjacent Mexico, was referred to as "*Apium* sp." in Contrib. 1, Estudios sobra Proderas Naturales del Uruguay, 1938 (p. 81), and some of the localities are indicated on a map in Contrib. 3, 1943 (p. 264). Of the North American species, it most nearly approaches *A. Popei* Torr. & Gray and *A. giganteum* Coult. & Rose, but differs from both in having the carpophore divided to the base, in its reddish-brown and less roughened fruit, and in the form of the incurving corky appendages of the lateral wings. It is a pleasure to name the species for Señor Bernardo Rosengurtt, whose collections have so greatly enriched the representation of Uruguayan plants in several North American herbaria, and who is also a discerning student of the genus *Eryngium*.

In general habit, the new *Ammoselinum* is startlingly similar to the illustrations of *Spermolepis Castellanosii* Pérez-Moreau (Pérez-Moreau, 1940, *fig. 1*) and of *Oligocladus patagonicus* (Speg.) Pérez-Moreau (Pérez-Moreau, 1936, *fig. 5*). From the external and transverse-sectional views of the fruits, however, it is clear that none of the three species is congeneric with either of the others, although we have not been able to examine any material of the *Spermolepis*. The fruit of *Oligocladus* is flattened dorsally at maturity and the scarcely compressed ovaries of immature plants are pubescent. Hence, we are inclined to accept *Oligocladus*, at least provisionally, as a valid genus of Peucedanoid affinities. The fruit of *Spermolepis* is compressed laterally, lacks well-defined ribs—the whole pericarp being tuberculate-muricate—and bears a conical stylopodium. Finally, the fruit of *Ammoselinum* is also laterally compressed, has prominent, acute, scabrous or callous-toothed ribs, the lateral ribs bearing prominent incurving corky appendages, and a low-conic stylopodium.

Arracacia Meyeri Math. & Const., sp. nov. Herba ampla infra inflorescentiam ramosa glabra e radice crassa, ca. 6 dm. alta; folia in ambitu ovato-triangularia, 1–2 dm. longa, 1–2 dm. lata, ternata deinde 1–2-pinnata, foliolis ovato-lanceolatis, apice acutis basi truncatis cuneatisve, 1.5–3 cm. longis, 0.5–2 cm. latis, inaequaliter grosse serratis plus minusve pinnatifidis, distinctis vel confluentibus, petiolulatis vel subsessilibus; petioli graciles 4–7 cm. longi basi late vaginantes; folia caulina pauca similia, petioli totis ad laminas vaginatis, laminis summis reductis; pedunculi graciles verticillati 6–8 cm. longi; involucelli bracteolae 1 vel 2 lineares 1–3 mm. longae; radii 5–8 graciles patenti-adscendentes, 2.5–3.5 cm. longi; pedicelli fertiles 1–6 patenti-adscendentes ca. 5 mm. longi; flores nobis ignoti; stylopodium depressum indistinctumque, stylis gracilibus patentibus, ovario glabro;

carpophorum verisimiliter bipartitum; fructus fusiformi-oblongus, 10–12 mm. longus, 2.5–4 mm. latus, glaber, ad basin versus fastigiatus apice truncatus, costis prominentibus acutis; vittae magnae in valleculis solitariae, in commissuris 2; semina sub vittis canaliculata facie sulcata.

Stout, caulescent, unbranched below the inflorescence, from a thick root, about 6 dm. high, glabrous throughout; leaves triangular-ovate, 1–2 dm. long and broad, ternate, then 1–2-pinnate, the leaflets ovate-lanceolate to

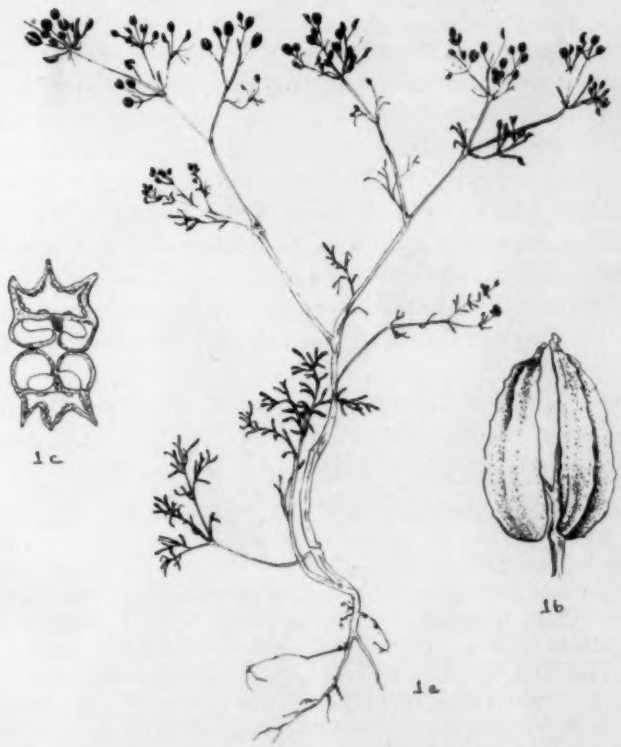

FIG. 1. *Ammoselinum Rosengurttii*. a. Habit, × ½. b. Lateral view of mature fruit, × 7½. c. Transverse section of mature fruit, × 8.

lanceolate, acute at the apex, truncate or cuneate at the base, 1.5–3 cm. long, 0.5–2 cm. broad, coarsely serrate and more or less pinnatifid, distinct, to confluent, petiolulate to subsessile; petioles slender, 4–7 cm. long, broadly sheathing at the very base; cauline leaves few, like the basal, the petioles wholly sheathing, the blades of the uppermost greatly reduced and linear; inflorescence a whorl of slender branches, each ending in a terminal umbel, the peduncles slender, 6–8 cm. long; involucre wanting, or of a single minute bract; involucel of 1 or 2 minute linear entire bractlets 1–3 mm. long, much shorter than the flowers; fertile rays slender, 5–8, spreading-ascending, subequal, 2.5–3.5 cm. long; fertile pedicels 1–6, spreading-ascending, about 5 mm. long; flowers unknown; stylopodium indistinct and depressed, the

styles slender, spreading, the ovary glabrous; carpophore apparently 2-cleft, fruit oblong-fusiform, 10–12 mm. long, 2.5–4 mm. broad, glabrous, tapering at the base, somewhat truncate at the apex, the ribs moderately prominent, acute; oil tubes large, solitary in the intervals, 2 on the commissure; seed deeply channeled under the tubes, the face sulcate.

TYPE: MEXICO. NUEVO LEÓN: In dense pine woods, alt. 3,000 m., Cerro del Viejo, Sierra Madre Oriental, 15 miles west of Dulces Nombres, Municipality of Zaragoza, 18 August 1948, *Meyer and Rogers 2970* (MO; LA, UC-photos).

Arracacia, a large New World genus with some 24 species in Mexico and Central America and nine others in northern South America (Constance, 1949), is readily divisible into two groups, primarily on the basis of the development of the stylopodium. The new species falls into the series with an indistinct and depressed stylopodium and apparently finds its closest affinity in *A. Schneideri* Math. & Const. which occurs in the same general region. It differs from this species in its smaller and more slender stature, glabrous rather than puberulent herbage, pinnatifid rather than merely serrate leaflets, more slender but shorter petioles, more slender peduncles, less conspicuous involucels, fewer and more slender rays, and longer and narrower fruit.

The species is named for its co-discoverer, Dr. Fred G. Meyer of the Missouri Botanical Garden, whose collecting trip into northeastern Mexico yielded a very rich harvest in a number of plant groups.

Podistera yukonensis Math. & Const., sp. nov. (fig. 2.) Herba acaulescens caespitosa, 10–15 cm. alta; folia numerosa erecta vel ascendentia, ovalia usque ad anguste oblonga, 3–6 cm. longa, 1.5–2 cm. lata, pinnata folioliarum paribus 3–6 oppositis orbiculatis vel anguste lanceolatis apiculatis, paribus infimis ternatis, ceteris indivisis, nervis marginibusque scabriusculis, petiolo 3–6 cm. longo, basi anguste vaginato; pedunculi plures crassiusculi angulati, 10–12 cm. longi, folias paullo superantes; involucri bractea integra unica vel plures an interdum defecens; involucelli bracteolae ca. 5 subdimidiatae acuminato-lineares integrae purpurae, 2–5 mm. longae, basi valde connatae; radii 4–8 crassiusculi aliquanto compressi 1.5–3 mm. longi; flores nobis ignoti; calyci lobi ovati evidentes; stylopodium conicum, stylis gracilibus recurvatis; fructus ovali-oblongus a latere compressus, ca. 3 mm. longus, 1.5 mm. latus, costis filiformibus prominentibus; mericarpiarum sectionibus transversis dorsaliter compressis; vitta sub costa quaque solitaria, in commissuris duae.

Plants 10–15 cm. high, acaulescent, cespitose; leaves numerous, erect or ascending, oval to narrowly oblong, 3–6 cm. long, 1.5–2 cm. broad, pinnate with 3–6 pairs of opposite orbicular to narrowly lanceolate, apiculate leaflets, the lowermost pair or pairs ternate, the others entire, the terminal often confluent, 6–15 mm. long, 1.5–5 mm. broad, scaberulous on the veins and margins, the petiole 3–6 cm. long, narrowly scarious-sheathing at the base; peduncles several, stout, angled, 10–12 cm. long, slightly exceeding the leaves; involucre of 1 or more small linear, entire bracts, or wanting (?); involucel subdimidiate, of about 5 linear-acuminate, entire, purplish bract-

lets 2–5 mm. long, connate at the base, about equaling the flowers and fruit; rays 4–8, 5-10 mm. long, stout, flattened and sometimes fasciated, ascending; pedicels stout, 1.5–3 mm. long, somewhat flattened; flowers unknown; calyx teeth ovate, conspicuous; stylopodium conic, the styles slender, recurved; fruit oval-oblong, ca. 3 mm. long, 1.5 mm. broad, compressed laterally, the ribs filiform but prominent; mericarps slightly flattened dorsally in transverse section; oil tubes solitary under each rib, 2 on the commissure.

TYPE: CANADA. YUKON: East-facing talus slope (very unstable), south side of Little Klondike River, at 5000 feet elevation, McQueston Area: lat. 63–64 N. and long. 136–138 W., 4 August 1948, *John D. Campbell 692* (CAN; UC-fragment).

FIG. 2. *Podistera yukonensis*. a. Habit, × ½. b. Lateral view of mature fruit, × 10. c. Transverse section of mature fruit, × 15.

The new *Podistera* differs sharply from the other three species of the genus in having the oil tubes solitary under the prominent fruit ribs, instead of more than one in each of the intervals. Its scaberulous foliage with entire leaflets resembles that of the Californian *P. nevadensis* (A. Gray) S. Wats., while the general habit and well developed rays and pedicels are more like those of the Coloradan *P. Eastwoodiae* (Coult. & Rose)

Math. & Const. and the Alaskan *P. Macounii* (Coult. & Rose) Math. & Const. Even in general aspect, however, *P. yukonensis* stands out as a remarkably distinct entity.

Hultén (1936) has pointed out that *P. Macounii* is, in his opinion, conspecific with *Ligusticum mutellinioides* (Crantz) Villar of arctic-alpine Eurasia. We do not have available sufficient material to make up our own minds on this point. Even though it be true, however, the group of species we have assigned to *Podistera* (Mathias & Constance, 1942) differs so markedly from the American species of *Ligusticum* that we hesitate to combine the two genera. A complete re-interpretation of *Ligusticum* must depend largely upon an intensive study of the eastern Asiatic representatives of the genus, which are very poorly understood. For the present, we think it advisable to retain the generic separation of the American species enumerated above.

Prionosciadium crinoideum Math. & Const., sp. nov. Herba crassa, 1 m. alta, apud inflorescentiam scaberula; folia basilaria incognita; folia caulina inferiora in ambitu ovata, 5–10 cm. longa, biternata, foliolis linearifiliformibus rigidis, apice abrupte acutis, 0.5–5 cm. longis, integris; petioli graciles, 15–30 cm. longi, basi vaginantes; folia summa caulina reducta, vaginis prominentibus; inflorescentiae umbella unica pedunculis terminalibus interdum lateralibus instructis; pedunculus 10 cm. longus, apice scabriusculus; involucri bracteae plerumque 6–8 lineares acuminatae 10–20 mm. longae; involucelli bracteolae 6–8 lineariae acuminatae 5–8 mm. longae; radii fertiles circiter 10 patenti-adscendentes subaequales apice scabriusculi, 2–3 cm. longi; pedicelli fertiles 2–8, 5 mm. longi; flores albi; fructus ovatus basi retusus, apice rotundatus, 7–8 mm. longus, 4–5 mm. latus, glaber, dorsaliter valde compressus, costis dorsalibus anguste alatis, lateralibus latius alatis, alis corpore angustioribus; vittae magnae in valleculis solitariae, in commissuris duae; semina sub valleculis canaliculata facie plana.

Plants stout, perhaps 1 m. high, the foliage glabrous, the inflorescence scaberulous; basal leaves unknown, the lower cauline leaves ovate, 5–10 cm. long, biternate, the divisions linear-filiform, rigid, quadrangular, abruptly acute, 0.5–5 cm. long, entire, the petioles elongate, 15–30 cm. long, sheathing at the base, the uppermost cauline leaves reduced, the sheaths prominent; inflorescence of a terminal and apparently one or more axillary peduncles, the terminal peduncle about 10 cm. long, scaberulous at the apex; involucre of about 6 linear, acuminate bracts 10–20 mm. long; involucel of 6–8 linear, acuminate bractlets 5–8 mm. long, longer than the flowers but shorter than the fruit; fertile rays about 10, spreading-ascending, unequal, 2–3 cm. long, scaberulous; fertile pedicels 2–8, about 5 mm. long; calyx teeth apparently obsolete; flowers white; fruit ovate, rounded at the apex, retuse at the base, glabrous, 7–8 mm. long, 4–5 mm. broad, the dorsal ribs narrowly winged, the lateral broadly winged, the wings narrower than the body; oil tubes large, solitary in the intervals, 2 on the commissure; seed channeled under the intervals, the face plane.

TYPE: COLOMBIA. MAGDALENA: Páramos of the Sierra Nevada de Santa Marta, about 30 miles inland from Dibulla; altitude about 3850 meters, July 1932, *W. Seifriz 493* (US No. 1,572,286; GH, LA, UC-photos).

The genus *Prionosciadium*, with some 16 species in Mexico and Guatemala, has been attributed to South America solely on the basis of juvenile material collected by Sodiro (No. *23*) in Ecuador, "sine loco et tempore, culta, origo incerta," the type of *P. Sodiroanum* H. Wolff. The type specimen (as indicated by the available photograph) is so immature that its assignment to any one of a half-dozen other genera might be argued with equal cogency. Superficially, it is reminiscent of a huge plant of *Foeniculum vulgare* Mill. with exaggerated cauline sheaths. Any critical appraisal of the entity will have to await additional collecting.

Prionosciadium crinoideum is closely comparable in fruit to several of the North American species, but the bizarre foliage immediately sets it apart from all of them. This constitutes an addition to the growing list of Mexican and Central American genera which are being found to occur in northern South America.

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TORREYA

FIELD TRIP REPORTS

Aug. 28, 1949. Beach Haven and Tuckerton, N. J. Everything that we hoped to observe was located this year including the marbled godwits seen for the first time, on our trip, since 1946. Excellent views of two splendid individuals were obtained on the Holgate mud flats, along with numerous other shore birds. Common terns and least terns were still feeding their young on the beaches. Among the thirty-six species of birds identified were the American egret, clapper rail, willet, great black-backed gull, Forster's tern, black tern and black skimmer. The sea lavender, swamp rose mallow and sea pink were all in bloom (both the pink and white forms of the latter were found among the blades of *Scirpus* and *Carex*). Attendance 7. Leader, David Fables.

Sept. 3–5. Pine Barrens, N. J. The group assembled at Merrygold and proceeded to Speedwell where general flora and historical ruins were seen. Near Pineworth, an early-blooming pine barren gentian and *Erianthus* enforced a stop along the highway. Batsto was visited for *Breweria* and *Isoetes braunii*. Here an ancient grist mill was inspected. At lower Bank a marsh rich with floral specialties, lying beyond the Charles Bell farm, was a surprise. On Sunday the remarkable pine barren bog at Oceanville was visited. At Absecon Mr. Lee Ellison was attracted by a thin film of blackish grains which by process of natural leaching had attained the surface of a roadside fill. He reports 26% titanium oxide in the substance. Few perhaps realize that this area is far from lacking in unusual minerals if one knows the secrets of locating them. Mr. Arthur O'Neil of Bargaintown entertained the group for an hour. His private museum was inspected, and a walk was taken through the woodland and swamp area which he so carefully maintains. A mockingbird was spied here by some of the party. Following the evening meal the shell piles at Longport were visited by moonlight. The two species of hermit crabs and the ghost crabs which may be seen here apparently had gone to bed. Attendance 13. Leader, Hollis Koster.

Sept. 10–11. Bennett Bog, N. J. A most successful trip ornithologically and botanically with but one disappointing feature—the early blooming of *Habenaria nivea* left only a portion of one plant in bloom on Sept. 10. Originally, the entire week-end had been built up around the blooming of *Habenaria nivea* which had been in bloom on these dates the past three years. The prolonged drought caused the season to advance considerably, and the plants were at the height of their bloom in mid August this year. The other expected species were more accommodating and were found blooming abundantly. The downy lobelia, bottled and pine barren gentians, rattlesnake master, nodding and grass-leaved lady's tresses, *Sclerolepis*, aster-like Boltonia, umbellate-leaved pennywort, white-bracted boneset and numerous other interesting plants were identified. The egret roost at Stone Harbor was visited the evening of the tenth, and most of birds counted as they came in from the marshes made golden by the rays of the setting sun. The total count was 1476 birds including 16 snowy egrets, 292 American egrets, 2 Louisiana herons, 991 little blue herons and 175 black-crowned night herons. At Cape May Point on Sunday the eleventh, a moderate hawk flight developed, approximately 80 sharp-shinned hawks were seen, as well as 3 Cooper's hawks, 3 bald eagles, 3 pigeon hawks and 4 ospreys. Three mockingbirds were also seen at Cape May Point. The presence of these birds always makes one feel as if he or she is in the deep south instead of a few hours ride from New York City. We were joined by members of the New Jersey Audubon Society, the Witmer Stone Bird Club and the Cape May Geographical Society. Attendance 125. Leader, David Fables.

Sept. 18. Cheesequake State Park, N. J. Areas visited: A. Borton Spring and salt marsh between it and Bell Point, also tip of Bell Point. B. Roadside south and west of former site of Booth Lake. C. Trail adjacent to and passing by "site" of booth Lake for some distance. D. Booth Lake Basin. E. Roadside east of Thomas Pond. F. Margins and head of Thomas Pond also small brook feeding it. Forty seven new plants were observed and their locations noted. This fine list of new species found was due to the nice "turnout" of "keen observers" including five members of the field committee. This brings the list of different species of plants observed on sixteen Torrey trips to four hundred and seventy nine. Attendance 15. Leader, L. E. Hand.

Oct. 2. Sim's Place, N. J. The interest in the barrens seems to by dying for the attendance was very poor. The bogs showed the effects of the dry weather. One noticeable thing was the tendency of spring flowers to bloom. Nice blooms of sand myrtle were found. Attendance 6. Leader, V. L. Frazee.

Oct. 16. Cushetunk Mountain, near Lebanon, N. J. Mr. Cantlon took the group up the north slope of Cushetunk Mt. and part way down the south slope. He discussed the results of his vegetation study there and pointed out many of the distinguishing features of the north slope vegetation as compared with the south slope. He also demonstrated his instrument installations with which he has followed the microclimate structure on the two sides of the mountain during the past two years. Attendance 12. Leader, John Cantlon.

Oct. 23. Appalachian Trail on Kittatinny Mts. N. J. Starting at the point known as Millbrook Road south, blazes were repainted along the road to the place where trail again strikes northeasterly and thence along the ridge crest to the opening overlooking Fairview Lake. The remaining half mile will be attended to next year. Two fallen logs were removed and much scrub was cut off the footway. The seriousness of last summer's drought was emphasized by the anhydrous condition of our spring. The worth whileness of our work was apparent when we met a party of hikers from Philadelphia completing a two day trek from Culvers Gap to Delaware River. Botanical observations were largely confined to admiring the autumn color. An occasional flower on plants of the pale corydalis and the lambkill reminded us of the diffculty some plants have in distinguishing early autumn from late spring. Attendance 22. Leader, John A. Small.

Oct. 30. Bushkill Falls, Pa. The members and guests assembled in the mist and rain of an autumn Sunday morning to continue the study of the rich bryophyte flora of this region begun in previous years (See Torreya **40**: 175–177; **41**: 136–137; **42**: 141–142). The prolonged drought of the past summer visibly affected the liverworts and mosses but little, for they never looked more vigorous or more abundant. Possibly the dryness which induced the dropping of the leaves or the death of aerial parts of some of the flowering plants actually made conditions more favorable for the growth of the bryophytes. On the damp soil along the banks and paths above the falls *Diplophyllum apiculatum* and *Microlepidozia sylvatica* serve as pioneers in succession, and actually are taking over; on the rocky slopes *Scapania nemorosa* and *Jubula pennsylvanica* play a similar role. In the low swamp area northeast of the falls, a number of liverworts were found that had not previously been recorded: *Odontoschisma denudatum* with its conspicuous clusters of gemmae at the apex of the stem, *Radula complanata* with its discoid gemmae making the leaf margins appear denticulate under a hand lens, and *Cephalozia connivens*. *Frullania* with conspicuouosly developed male "inflorescences", in addition to the female branches, was found. *Frullania plana* had not been identified here before. The tree moss, *Climacium*, grew sparingly along the stream banks. Numerous other liverworts and mosses, noted in other years, were seen again, such as *Pellia, Reboulia, Lejeunea, Leucolejeunea, Tortella* and *Thelia* and *Rhodobryum* in abundance, *Fontinalis gigantea, Buxbaumia sphylla* et al. In the afternoon *Woodsia ilvensis*, the "Rusty cliff-fern" was found growing in the crevices of the rocks west of the main falls. The spring and stream to the northwest yielded *Geocalyx graveolens* with its unusual "perigynia", and *Anthoceros*

laevis growing close to the *Marchantia*, *Conocephalum* and *Riccardia* collected in previous years. Fourteen members left just as the gates were closed at five o'clock, to return through the fog and rain. The day was dismal, but the liverworts and mosses looked unusually cheerful. Attendance 26. Leader, Edwin B. Matzke.

Nov. 6. Lakewood, N. J. In the absence of Mr. Frazee, Mr. Murphy led the group for a very pleasant trip around the lake and the cranberry bog. No rare plants were found, but several puff balls were seen, including *Calvatia cyathiformis*. Attendance 10.

Nov. 13. Watchung Reservation, N. J. The leaders planned the trip as a study of the hemlock grove as representative of the status of the hemlock in north central New Jersey. At four points in the course of the trip the leaders asked a series of questions. Part of these they answered, some the party sought answers to themselves, some are still unanswered. They dealt first with the general orientation of this hemlock grove in the range of the species, secondly, with the present status of hemlock in the Reservation, thirdly, with the future of the hemlock community there, fourthly, the relation of the hemlock to the other communities of the Reservation, and finally the future of the whole Reservation as an ecological unit. Attendance 28. Leaders, Mrs. George Anderson, J. E. Cantlon, and M. F. Buell.

Nov. 20. Swimming River near Red Bank, N. J. The first stop was just outside of Red Bank near where the Swimming River joins the Navesink estuary. Our main purpose was to see the hemlocks. They were found on the steep slopes of a bluff facing in a generally northward direction. They were numerous, though it could hardly be said that the hemlocks alone formed a closed canopy. A rapid census enumerated some thirty species of plants identifiable at the season. Cherry birch and beech were conspicuous. Hemlock seedlings were found on the level land at top of slope but no saplings or large trees there. Trees on the slope were up to 20 inches d.b.h. The second stop, near Phalanx, yielded a good stand on north side of a point where the Swimming River forked. There appeared to be ample reproduction here and all sizes could be found, even up on the level land. Tupelo (*Nyssa*) replaced the cherry birch as a conspicuous associate with the hemlock and beech. This stand appeared to be the most extensive and of greater density of hemlock than the other two. The third stand was along Route 34. It faced northward, overlooking Yellow Brook a tributary of Swimming River. The area had been highly protected for ten years and somewhat modified by the owner, even to the extent of some planting. The slope here was less steep and not as high as the others. The stand was fairly dense along the brook, soon becoming mixed. What appeared to be natural reproduction extended back to the property line where its abrupt termination may have been due to the practices of man. Red maple and beech were among the associated plants. To those of us acquainted with the hemlock ravines on the piedmont and northward, these stands on the coastal plain were highly interesting. Should we call these places ravines? Should we call these plant communities associations? Or relic colonies? How extensive had the hemlocks been in the original forests adjacent? How had they escaped the axe and fire? How did they get there in the first place? How long have they been there? Did they survive the postulated xerothermic period of post glacial times? Attendance 14. Leader, V. L. Frazee.

BOOK REVIEW

Natural History of Danish Lichens. By Olaf Galløe. Einar Munksgaard, Nörregade 6, Copenhagen. 40 Kr. per vol.

Growing out of two decades of work on the ecology of lichens in Denmark and Iceland, Galløe was impressed with the lack of detailed descriptions of individual lichens, as most systematists have based their descriptions on data taken from several specimens which may or may not be identical in structure, paying most attention to characters which

the author thought most important for classification. Galløe has attempted to fill this gap in our knowledge in the work under review.

His method has been to study an individual carefully in all its parts, then to identify it with a full description of a previous author, usually Th. M. Fries, *Lichenographia Scandinavica*, 1871–4, expressing no opinion on Fries' synonymy nor of the possibility of an older, less well described species. Variants, ecologic or others, which come within the limits of Galløe's species concept, are then carefully described, but not named. The work is amply illustrated with drawings of habit, details of thallus and apothecium, some colored, others in black on white, e.g. *Lecidea elaeochroma* covers 30 plates. Chemical reactions are briefly discussed, but are not relied on as much as by some other workers. Galløe considers the reaction with KOH as the most useful and records it when it is positive.

The first volume of 93 pp. with 388 figures on 160 plates deals with the genus *Lecidea*. His discussion of phylogeny states broad fundamental principles which are applicable to most other large crustose genera. He then discusses the morphology and development of the thallus and apothecium, the physiology and the ecology of the Danish species, especially the factors responsible for morphological changes.

The second volume of 84 pp. with 416 figures on 128 plates and the third volume of 114 pp. with 345 figures on 127 plates treat the remaining genera of the Lecideaceae and some small genera, sometimes classified elsewhere, which have many characters suggestive of those of the Lecideaceae.

The fourth volume of 81 pp. and 559 figures on 133 plates deals in the same thorough manner with *Buellia*, *Catolechia* and *Lecanora*.

The fifth volume of 117 pp. and 728 figures on 140 plates deals with the remaining genera of the Lecanoraceae, *Pertusaria*, *Caloplaca*, *Gyalecta*, *Diploschistes*, *Thelotrema* and *Rinodina*.

The sixth volume of 103 pp. with 541 figures on 88 plates deals with the families of lichens having Myxophycean algae as symbionts.

The seventh volume of 72 pp. with 657 figures on 101 plates deals with the Parmeliaceae and *Xanthoria*.

While the work is still incomplete and not provided with keys for rapid identification of specimens, it is a mine of information on the morphology and ecology of the Danish species, since the descriptions are complete for characters and structures usually overlooked by many systematists. The discussions of phylogeny are excellent and repay careful reading by anyone working on the genera so far treated.

In some of the essentially tropical and subtropical genera which are represented in Denmark by a single species, the work suffers from lack of knowledge of the morphology of the rest of the species in the genus, but in view of the time-consuming work that has gone into the preparation of these volumes, it is obvious that the author has been unable to study many exotic species. Whatever changes in nomenclature or classification may occur in the next century, this work will survive as a fundamental contribution to our knowledge of this interesting group of plants. Botanists will look forward eagerly to the remaining volumes of this work.—Carroll W. Dodge.

NOTE: Lichen students around New York will find a set of these books at the New York Botanical Garden Library.

NOTES

United Nations (Department of Social Affairs) has launched a new periodical, named BULLETIN ON NARCOTICS. The first issue contains an article on "Determining the origins of opium," and a report on "The commission of enquiry on the coca leaf." Both papers contain much of interest to botanists, particularly to students of economic botany.—H. W. R.

Alice Lounsberry, well known for many popular writings in botany, died on Sunday, November 20, in New York. She was born in the same city on 6 November 1872. Besides a number of articles in the popular press, she wrote a GUIDE TO THE WILD FLOWERS (1899), GUIDE TO THE TREES (1900), SOUTHERN WILD FLOWERS AND TREES (1901), THE WILD

FLOWER BOOK FOR YOUNG PEOPLE (1906), THE GARDEN BOOK FOR YOUNG PEOPLE (1908), GARDENS NEAR THE SEA (1910).—H. W. R.

Charles Alfred Weatherby. The sudden death of C. A. Weatherby came as a bitter blow to all those who had known him, either through personal contact or correspondence. Professor M. L. Fernald, his long-time co-worker at the Gray Herbarium, has given us an excellent account,[1] hence there is no need to review here the details of Weatherby's life and career.

When, in 1946, the writer of these notes was faced with the selection of a small central committee on nomenclature of the American Society of Plant Taxonomists, there was never any doubt but that Weatherby was a most desirable person to have associated with the work, primarily in the role of "elder statesman" who could act as guide and counselor. The first task of this committee was the compilation of a special edition of the International Rules of Botanical Nomenclature,[2] then unavailable in printed form and scattered in various places.

None of the committee envisioned what was to transpire when it later called for proposals for changes in the Rules; the response literally swamped its members for a full year. The members of this committee examined each proposal and then made individual reports to each other and, ultimately, to the proposer, on its basic value and "workability." In this activity the keen and analytic mind of Weatherby really came into play. The committee's correspondence was vastly more voluminous than the proposals themselves and there was scarcely a week passed during the year that bulky packets of comments and suggestions for improvement of proposals did not pass between us.

There are some who have always thought of Weatherby as being one to avoid controversy. Certainly this was not true where nomenclatural matters were concerned. His attack, however, was misleading, for it was not that of a Neanderthal wielding a bludgeon; instead it was that of a most refined and civilized gentleman fully skilled in the use of a rapier. It has always seemed unfortunate that the very best of these comments were necessarily omitted in the impersonal, mimeographed report wherein it could be stated only of certain proposals that they were "not approved by the Committee," followed by a much condensed summary of the reasons. These remarks would have made choice reading and would have been of great interest and value to a whole generation of taxonomists.

Yet there was one characteristic of Weatherby which stood out through this whole work:—his insistence that both sides of a really controversial question be submitted for consideration. Because of this, on occasion either he, or other members of the committee, were moved to make proposals for which we had little personal regard. The broad scope and balance of the proposals can largely be laid to his vigilance and fairness. It will always be a source of personal regret that Weatherby passed from us just a few days before these proposals, in final form, appeared in print.[3]

Weatherby's spirit of impersonal fairness appeared in other ways. He and I had various heated discussions regarding possible nomenclatural changes at some time in the future necessary to accommodate the findings of the experimental taxonomists. Personally he saw no need for them, yet when he somehow learned that a coming symposium purporting to examine nomenclatural problems had been so arranged as to exclude discussion of the needs of the experimentalists he wrote me a memorandum in which he was obviously highly incensed. Only on one other occasion did he use certain four-letter Anglo-Saxon expletives in his extended correspondence with me. I heard nothing more of it until he personally appeared on this same symposium. The closing clauses of his argument, wherein he points out what still remained to be done to the Rules—". . . and, should that prove necessary, in accommodating our ways to the results of experimental

[1] Rhodora **51**: 169–179. 1949.

[2] Camp, W. H., Rickett, H. W., and Weatherby, C. A. International Rules of Botanical Nomenclature. Brittonia **6**: 1–120. 1947. Second printing; Chronica Botanica Co., 1948.

[3] Camp, W. H., Rickett, H. W., and Weatherby, C. A. Proposed changes in the International Rules of Botanical Nomenclature. Brittonia **7**: 1–51. 1949.

taxonomy''—followed by a most pertinent quotation from De Candolle, was his reply to those who had sought to exclude the experimentalists from the field of discussion.[4]

There was no need for him to go beyond the bounds of his purely historical topic. Yet he did just this. Knowing him so well I feel certain that it was done solely that the experimentalists might have a voice before the court. As Professor Fernald points out in his account, Weatherby was a literary scholar before he turned to botany; consequently, he was fully aware of the exact meaning of the words he used and the inferences to be drawn from his sentence structure. It was therefore doubly astonishing to find in that summarizing sentence closing phrases, thrust home with the lightning flash of his verbal rapier, which contained a most unexpected prophecy. Certainly, it is of more than passing interest to note that he did not say that the experimentalists would have to follow the edicts of the classical taxonomists in matters nomenclatural; instead, he clearly intimated that, where necessary and when the time was ripe, the classical taxonomists would be the ones who would have to accommodate their ways to the results of experimental botany.

This scholarly ability to see both sides of a question resulted in another characteristic reaction. At a time when certain New England botanists were in open and acrimonious feud with a group of New York botanists, Weatherby not only joined the Torrey Botanical Club, its membership then almost limited to persons within the New York area, but also became a Life Member. This gesture can be an example to all of us, for his name on the rolls of the Club will stand forever as a shining example of the impartiality and clear-headed thinking of a true scientist and philosopher.—W. H. Camp.

Neil E. Stevens 1887–1949. Neil Everett Stevens was born April 6, 1887, at Portland, Maine. In 1914 he married Maude Bradford. To them twin sons and a daughter were born. Dr. Stevens received an A.B. degree from Bates College in 1908, and a Ph.D. degree from Yale University in 1911. During his professional career he was employed by Kansas State College as an Instructor, the Bureau of Plant Industry of the United States Department of Agriculture as a Pathologist, and the University of Illinois as Professor of Botany and Plant Pathology. He died June 26, 1949.

In Dr. Stevens' death American phytopathology lost an excellent teacher and one of its most dynamic investigators. For a period of more than thirty-five years he devoted most of his time and great energy to problems connected with crop losses by American farmers. His chief contributions were on diseases of chestnut, strawberry, cranberry, currant and corn. Special attention was given to fungi causing chestnut blight, fruit rots of strawberries and cranberries, and corn ear rots. He made many contributions to knowledge of the bacterial infection responsible for Stewart's disease of corn and the virus malady, cranberry false blossom. He studied the effects of climatic conditions, especially temperature fluctuations, on prevalence and severity of several different diseases. A series of forecasts of damage by Stewart's disease of corn was an outstanding feature of this work. When investigations on cranberry false blossom disease were undertaken by the Boyce Thompson Institute he travelled from Washington, D. C., to Massachusetts, and generously aided in a survey of the insect fauna of affected cranberry bogs in that State. He taught plant sciences in Kansas State College, George Washington University and the University of Illinois.

In spite of all these activities he found time to write papers on such diverse subjects as unusual methods of controlling plant diseases, history of botany in the United States, petrified palms, a Penicillium ''disease'' of ink, excessive meekness and politeness of American botanists, bureaucracy as a way of life, and many other subjects. By his publications, by personal contacts, in conversations and talks before numerous meetings, by serving as an officer in many different botanical organizations and by his teaching he influenced to an unusual degree the thinking of his colleagues in the United States Department of Agriculture and throughout the country. He was an inspiring teacher, a gifted writer, an entertaining talker, a critical experimentalist and a champion of new ideas. To the very end of life Dr. Stevens retained a youthful appearance and a youthful point of view.—L. O. Kunkel.

[4] Weatherby, C. A. Botanical Nomenclature since 1867. Am. Jour. Bot. 36: 5–7. 1949.

BULLETIN OF THE TORREY BOTANICAL CLUB
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TORREYA

Francis Bacon Lunches with the Torrey Botanical Club[1]

W. H. Camp

Upon receiving the invitation to speak before this group it was realized that there was an implication that if I so desired I could present to you some of the details of my present work. This might appear to have been an easy way out for, as you know, I am willing at all times to discuss the genetic structure of natural populations. This, however, would have involved the making of a series of diagrams and graphs. Therefore, being by nature a rather indolent fellow, I decided on another course—that of inviting an old friend to attend our luncheon and letting him do most of the talking.

I cannot remember just when it was I first made the acquaintance of Francis Bacon. Apparently, some time around the turn of the century, some fast-talking book agent sold my father one of those sets of books, so popular at the time, which contained the classic works of the past. It would be a gross untruth to say that I had read this full shelf of books; of the majority I remember little, except that their backs were a dark green. The set must have contained works in philosophy, literature, history, biography and, to some extent, in science, for I dimly remember such names as Aristotle, Plato, Shakespeare, Prescott, and Napoleon on them. Nor do I remember how much of science was represented. The only volumes which I can recall today with surety are Darwin's *Origin of Species* and *Descent of Man* and Francis Bacon's *Novum Organum*. This was strange and unseemly fare for a lad of no more than 13 or 14 years. It must have been then that I first read them for I distinctly remember the circumstances under which I read Lyell's *Principles of Geology*, which was the spring of my 15th year, and after I had read these works of Darwin and Bacon.

Now I would not have you think that a lad of that age would understand the implications of those great works. At least I do not claim to have done so. Whether any of the philosophy contained in them was unconsciously absorbed may be a moot question. All I know is that, subsequently, during my collegiate and graduate career I was able to turn to them with pleasure, since they already were old friends. During my college years, the rediscovered Mendelism had filtered downward into the beginning biology courses. Evolution was accepted, but the beautiful precision of the ratio of blue to white peas in the F_2 generation, when coupled with the mutations in de Vries' Oenotheras, permitted strong doubts to be cast on Darwinism. All that was needed was enough gross mutations, followed by genetic segregations, and we could explain evolution. We could take evolution as a general philosophy, but would kick Darwinism out the back door. Darwin had only been speculating, whereas we now had concrete evidence of what really takes place.

There is no need to recount, except for the youngest among us, the eagerness with which biologists generally seized upon the explanation, for its ability to rationalize a difficult problem set their minds at rest. Bacon had cautioned us of just this sort of situation, for he definitely warned that "The human understanding, when

[1] Remarks delivered at a luncheon meeting, December 29, 1949.

any proposition has been once laid down (either from general admission and belief, or from the pleasure it affords), forces everything else to add fresh support and confirmation; and although most cogent and abundant instances may exist to the contrary, yet either does not observe or despises them, or gets rid of and rejects them by some distinction, with violent and injurious prejudice, rather than sacrifice the authority of its first conclusions. . . . It is the peculiar and perpetual error of the human understanding to be more moved and excited by affirmatives than negatives, whereas it ought duly and regularly to be impartial; nay, in establishing any true axiom the negative instance is the most powerful."[2]

It has been interesting through the years to watch biologists wrestling with their consciences when they discovered that the "mutations" which had been found in *Oenothera* were not at all the things they had supposed, but were merely recombinations of old and already-present characters which did not appear in an expected Mendelian ration because of a series of balanced lethals. We still hold to the doctrine of change through mutations, but if one can judge from the mutterings and rumblings about us, their magnitude is rather closer to that which Darwin postulated than that of the de Vriesian mutationists.

Furthermore, I have been watching with increased interest the current results of certain spectroscopic analyses indicating the remarkable changes which take place in the nuclear substances during certain critical stages in cell division, at the time when duplicative genes may well be reconstituted. Is this the place where micromutations are initiated? If so, there is a possibility that environmental factors *might* sometimes play a part in modifying this delicately balanced and exceedingly complicated chemical process. I do not think that it is mere chance that the grosser mutations, with which we have so far been dealing, are best induced by artificial means at these same critical stages.

As a taxonomist, I have been interested in our guest's views on the classificatory activities of humans. He may not have written specifically on biological taxonomy as we know it today, yet his generalizations are of sufficiently wide application that they have value. Any man sufficiently astute to realize his place and limitations, and who understood his role to be that of the one who "rang the bell which called the wits together" deserves our attention. We have long been plagued with two schools of biological systematizers—the lumpers and the splitters. Of these, he remarks: "The greatest and, perhaps, radical distinction between different men's dispositions for philosophy and the sciences is, that some are more vigorous and active in observing the differences of things, others in observing their resemblances; . . . each of them readily falls into excesses, by catching either at nice distinctions or shadows of resemblance." [LV]

From this, one might infer that Bacon advises a middle course of action. I doubt it very much. He is not so much interested in points of philosophy as in the accumulation and interpretations of facts. He notes that he is "wont, for the sake of distinction, to call that human reasoning which we apply to nature the anticipation of nature (as being rash and premature), and that which is properly deduced from things the interpretation of nature." [XXVI] "Anticipations" he says, "are sufficiently powerful in producing unanimity, for if men were all to become uniformly mad, they might agree tolerably well with each other." [XXVII] In spite of the seeming disagreements of the lumpers and the splitters they did agree on

[2] *Novum Organum*, Book I; Aphorism XLVI. Note: Since all following quotations are from this source, the citation, in Roman numerals enclosed by brackets in the text, will refer only to the number of the Aphorism in Book I.

the one basic thing: that, in a manner of speaking, their species were biological compartments—mere boxes—to be considered as things apart from each other. Of course, one would not imply that our guest's aphorism could be rephrased so that the syllogistic conclusion would be reached that those who agree are necessarily "uniformly mad."

The last decade or so has witnessed a considerable change of attitude on the part of certain workers concerning many species. The sort of patient and costly experimentation which our guest advocates has recently been yielding rather confounding results. In spite of the neatly defined taxonomic compartments which we have constructed for our species, we are discovering that there are no lines between the so-called species in such things as the section *Onagra* of *Oenothera*. Among the stemless blue violets there is complete interfertility; this, when coupled with the biomechanics of the group, yields a most complicated series of races, but no neatly compartmented species such as we always have been told were there. One could go on at great length, citing instance after instance, where our former concept of the species is breaking down in the face of systematized experimentation with living populations.

The danger of adherence to a fixed formula of interpretation is fully understood by our guest for he has pointed out that "The human understanding, from its particular nature, easily supposes a greater degree of order and equality in things than it really finds; and although many things in nature be *sui generis* and most irregular, yet will invent parallels and conjugates and relatives, where no such thing is." [XLV] In the case of biological systematics this anticipation of order and equality is a direct hold-over from a belief in the doctrine of a special creation with its concomitant compartmentalization of the species.

A few years ago there was an attempt on the part of several of us to probe a little way into the mechanics of living populations.[3] One of the most difficult problems faced was the attempted rationalization of the species, as a philosophical entity, with the dynamic and ever changing populations which were being revealed by experimentation, and which refused to be compartmentalized under the old static concept. Those faced with the situation found it necessary to venture into new and uncharted channels of thought. The morphology, or form, of an organism previously had been the criterion used in deciding its relationship. The problem which had to be attacked was: Is form the criterion for the delimitation of species?; or, is the genetic mechanism of a living population more important? On this subject, our guest remarks: "The human understanding is, by its own nature, prone to abstraction, and supposes that which is fluctuating to be fixed. It is better to dissect than abstract nature. . . . It is best to consider matter, its conformation, and the changes of that conformation, its own action, and the law of this action or motion; for forms are a mere fiction of the human mind, unless you will call the laws of action by that name." [LI]

In analyzing these dynamic populations, the fixed compartments of the taxonomist's species often were found to be "a mere fiction of the human mind"; therefore the authors were led, in general, to take the combined genetic mechanics and gene structure of a population as the criterion upon which, primarily, its circumscription was to be based. This certainly was a departure from custom; yet it seemed warranted, since living organisms were involved and, therefore, that the "laws of ac-

[3] Camp, W. H. and Gilly, C. L. The structure and origin of species. Brittonia 4: 323–385. 1943.

tion" within them should determine how they were to be defined rather than any preconceived notion about the uniformity of their external morphology.

There are, no doubt, some who sincerely hope that the new approach to the systematics of living organisms can be grafted on the old, perhaps as a frill on the margin of orthodox taxonomy. I doubt if this is really possible for, as our guest points out, "It is in vain to expect any great progress in the sciences by superinducing or ingrafting new matters upon old. A [renovation] must be made from the very foundations, if we do not wish to revolve forever in a circle, making only some slight and contemptible progress." [XXXI]

If there were time to outline more fully the status of science and philosophy during the period when our guest was actively writing, we might better understand the constant quarrel with his contemporaries. Some theologians were still arguing over how many angels could dance on the head of a pin, chemists were still to be found in the smoky grottoes of the alchemist, and some botanists were still hunting for the clue to cures in their plants through the doctrine of signatures. Looking about he saw little else than chaos in what was then called science. This must be said for him: He did not despise such facts as already had been discovered; the thing which he regretted was the waste of time expended by the undirected and unorganized experimental methods which he observed about him. He argued, as well as any man might, that "We must not only search for, and procure a greater number of experiments, but also introduce a completely different method, order, and progress of continuing and promoting experience. For vague and arbitrary experience is (as we have observed), mere groping in the dark, and astonishes rather than instructs. But when experience shall proceed regularly and uninterruptedly by a determined rule, we may entertain better hopes for the sciences." [C]

One can imagine his inward indignation when he saw the pointless scurrying about of many of those who then called themselves scientists. One sometimes wonders, therefore, just what he would say if he were to drop into the laboratories of some of us and witness the numerous times when studies have been initiated with but little attention being paid to their place in the broader pattern of the body biologic. One hears all about the great cry that scientists must be left completely independent to pursue such studies as they will. I certainly do not hold that scientists should be restricted on the kinds of researches they pursue; such a policy would be fatal to science. However, I do hold that scientists, themselves, if they are to be worthy of the name, should at least be sufficiently realistic to look about them to ascertain whether their researches are directed toward a fundamental elucidation of the unknown, or are merely interesting exercises of the intellect. I doubt if Bacon implies that cost accounting should be done on independent research, but he realizes the great extent of the unknown and the need to have a definite plan of attack if the researches are to be conducted economically. This is shown by his clear statement that ". . . although it may now and then happen that one falls by chance upon something that had before escaped considerable efforts and laborious inquiries, yet undoubtedly the reverse is generally the case." [CVIII]

As a keen student of human nature, as well as of the philosophy of science, our guest also realizes the temptations which can diffuse our activities for he points out that ". . . there is such a multitude and host, as it were, of particular objects, and lying so widely dispersed, as to distract and confuse the understanding; and we can, therefore, hope for no advantage from its skirmishing, and quick movements and incursions, unless we put its forces in due order and array, by means of proper and well arranged, and, as it were, living tables of discovery of these matters, which

are the subject of investigation, and the mind then apply itself to the ready prepared and digested aid which such tables afford." [CII] And what are these "living tables of discovery" about which our guest tells us? They are the printed record of experimentation and scientific discovery.

It is quite obvious that our guest is no person to hide his own light under a bushel. Nor would he wish to see someone else cover their light. He seems firmly convinced that there can be no real advance in science unless the work of scientists is fully recorded and made available to all. No real scientist can work alone with his own experimentations; there must be a comparison with the data found before, a sharing of current data, and a recording of it for the future. "The human mind" he states, "is often so awkward and ill-regulated in the career of invention that it is at first diffident, and then despises itself. For it appears at first incredible that any such discovery should be made, and when it has been made, it appears incredible that it should so long have escaped men's researches. All which affords good reason for the hope that a vast mass of [knowledge] yet remains, which may be deduced not only from the investigation of new modes of operation, but also from transferring, comparing, and applying those already known, by the method of what we have termed literate experience." [CX]

I know of no better example of the practical implementation of "literate experience" than one of the major activities of the Torrey Botanical Club. The Club may have started as a small group coming together around John Torrey's pot-bellied stove to exchange experiences and the findings of its latest field trip, but it was not long after that the need was felt for its experiences and discoveries to be set down in permanent form. Thus began the scientific publication which later was to blossom into the internationally known and justly respected BULLETIN OF THE TORREY BOTANICAL CLUB. The Club's INDEX TO BOTANICAL LITERATURE is a further expansion of this "literate experience," as are the MEMOIRS and TORREYA.

One thing, however, remained undone. Within the 75 volumes of the Bulletin, there was locked up a staggering amount of botanical information which was in no way adequately listed by indexes to the separate volumes or, for that matter, by any other existing index. These volumes of the Bulletin cover one of the greatest transitionary stages in all the history of botany. Simple author and subject indexes would not suffice to uncover the hidden knowledge therein recorded. The proper treatment seemed almost impossible. Our guest today, therefore, will understand that the Club takes considerable pride in pointing out that we now are looking forward to the imminent completion of this monumental task and to the publication of an Index wherein will be indicated for ease of reference every technique and discovery, as an item in its own right, and the location of the name of every organism that has been dealt with critically in any portion of the biological discipline, or which appears in floristic lists, for every one of these 75 volumes.

Thus, through its various literate experiences, the Torrey Botanical Club keeps faith with the basic philosophy of a true and living science, enunciated with such clarity by our honored guest over three centuries ago.

THE ACADEMY OF NATURAL SCIENCES
PHILADELPHIA, PENNSYLVANIA

INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF THE TAXONOMIC INDEX

TAXONOMY, PHYLOGENY AND FLORISTICS

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(See also under Spermatophytes: **Le Gallo, C.**; under Ecology: **Rigg, G. B. & Miller, R. C.**)

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